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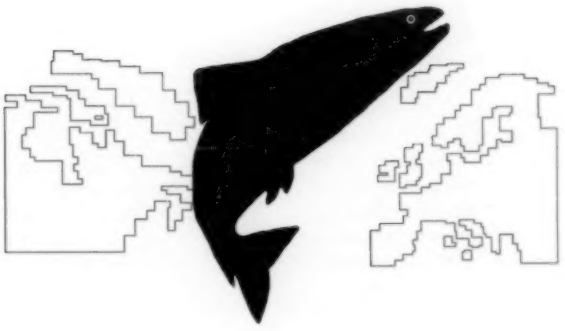

Integrating across scales: effectively applying science for the successful conservation of Atlantic salmon (*Salmo salar*)

Martha E. Mather, Donna L. Parrish, Carol L. Folt, and Richard M. DeGraaf

Abstract: Atlantic salmon (*Salmo salar*) is an excellent species on which to focus synthetic, integrative investigations because it is an economically important species that captures the public imagination, is heavily impacted by humans, uses several ecosystems over its life, and is the subject of a large body of extant literature. The following 24 papers were solicited to provide the biological basis for effective and innovative approaches that biologists, managers, and social scientists can use to develop policies that sustain Atlantic salmon and related species. Together these papers highlight the need for and benefits of (*a*) synthesizing within populations, (*b*) choosing the appropriate scale, (*c*) comparing across populations using rigorous, focused, question-oriented methods, (*d*) integrating across disciplines, (*e*) incorporating the human perspective, (*f*) linking multiple ecosystems, and (g) applied problem solving. To show how Atlantic salmon can guide research and conservation efforts for other species in other systems, we review the justification for the supplement and summarize the defining concepts that emerge from the volume.

Résumé : Le saumon de l'Atlantique (*Salmo salar*) est une excellente espèce pour la réalisation d'études synthétiques intégrant diverses composantes parce qu'elle a une importance économique et qu'elle intéresse le public, est fortement exposée aux impacts anthropiques, utilise plusieurs écosystèmes durant son cycle vital et fait l'objet d'une abondante littérature. Nous avons sollicité les 24 articles suivants pour présenter les bases biologiques qui peuvent s'avérer utiles dans l'élaboration de méthodes efficaces et novatrices que les biologistes, les gestionnaires et les spécialistes des sciences sociales pourront utiliser pour établir des politiques favorables au saumon atlantique et aux espèces apparentées. Ensemble, ces articles font état de la nécessité et des avantages des actions suivantes : (*a*) considérer les populations de façon synthétique, (*b*) choisir l'échelle appropriée, (*c*) comparer les populations au moyen de méthodes rigoureuses bien ciblées et fondées sur le questionnement, (*d*) faire appel aux diverses disciplines concernées, (*e*) incorporer la dimension humaine, (*f*) établir des liens entre les multiples écosystèmes, et (*g*) appliquer des processus de résolution de problèmes. Pour montrer comment le saumon atlantique peut guider les efforts de recherche et de conservation visant d'autres espèces et d'autres systèmes, nous revoyons la justification du présent supplément au journal et résumons les concepts clés qui émergent des articles.

Traduit par la Rédaction

Introduction

Great interest exists in effectively linking research conducted over multiple spatial and temporal scales to strategies that balance natural resource conservation with human development. Accomplishing this goal requires rigorous research methods together with an understanding of the role that humans play in the ecosystem. Atlantic salmon is an economically valuable species that captures the public imagination, is impacted by humans, uses several ecosystems over its life, and requires both small- and large-scale investigations. Thus, it is a model species for examining a variety of ecological questions, scale issues, human impacts, ecosystem processes, interdisciplinary challenges, and methodologies for problem-solving. Furthermore, much is known about Atlantic salmon from working within traditional scientific disciplines, specific geographic regions, and individual habitats. Scientific productivity relative to this species has been consistently high (Fig. 1*a*). Of the 1410 papers on Atlantic salmon identified by a literature search (1985–1994), all disciplines and life stages have been examined (Fig. 1*b*,*c*) although behavior and ecology (Fig. 1*b*) and the parr and smolt stages (Fig. 1*c*) were emphasized.

In spite of this extensive attention, most wild populations of Atlantic salmon are at risk. Specifically, of 25 regions within the original range of Atlantic salmon in North America and Greenland, only 11 are stable while five are declining, one is totally extirpated, and eight are being restored

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M.E. Mather.[1] Massachusetts Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, BRD Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003, U.S.A.
D.L. Parrish. Vermont Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, BRD, University of Vermont, Burlington, VT 05405, U.S.A.
C.L. Folt. Department of Biology, Dartmouth College, Hanover, NH 03755-3576, U.S.A.
R.M. DeGraaf. USDA Forest Service, Northeastern Research Station, Amherst, MA 01003, U.S.A.

[1]Author to whom all correspondence should be addressed. e-mail: mather@forwild.umass.edu

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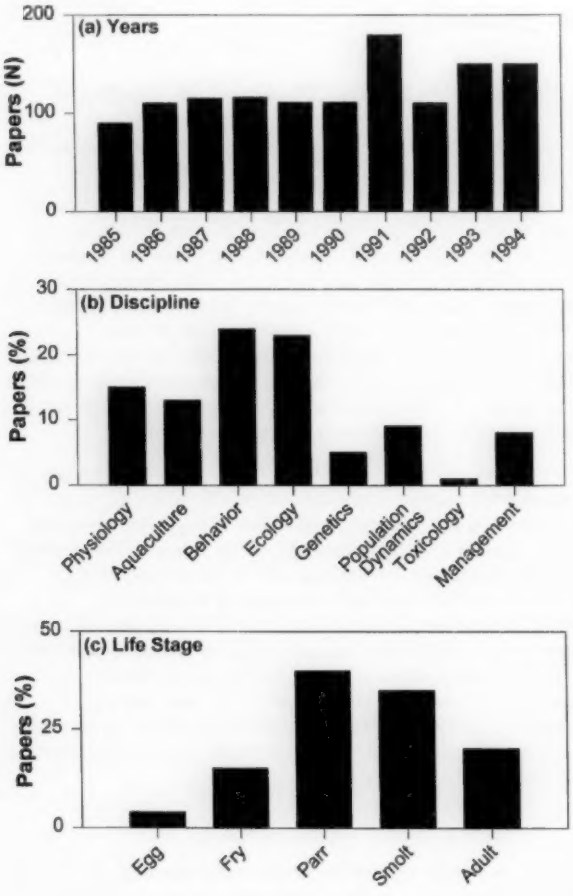
Fig. 1. Representation of peer-reviewed research papers from a search of a BIOSIS database using the keywords "Atlantic salmon" from 1985–1994 (*a*) across years, (*b*) disciplines, and (*c*) life stages.



after extirpation (Parrish et al. 1998). Similarly, of 28 regions within the original range of Atlantic salmon in Europe, only five are stable whereas nine are declining, seven are totally extirpated, and seven are being restored after extirpation (Parrish et al. 1998). Because two-thirds of the regions that contained Atlantic salmon historically have declining or extirpated populations, new information on Atlantic salmon is needed to aid future management efforts.

To contribute new scientific information that can help conserve Atlantic salmon, we solicited 24 papers that examine patterns and processes related to five broad topic areas: (*a*) life history; (*b*) space, food, and habitat use; (*c*) biotic interactions; (*d*) genetics; and (*e*) biophysical links and anthropogenic alterations (Table 1). Several crucial concepts arise from these papers. In particular, these papers emphasize: (1) the critical need to examine within-population trends at multiple temporal and spatial scales; (2) the novel perspective that arises from across-population synthesis; (3) the insights provided by integrating across multiple disciplines; (4) the need to explicitly incorporate human impacts into ecological research; (5) the value of linking multiple ecosystems; and (6) approaches to applied problem solving (Table 2). Each paper builds upon a synthetic review of the literature pertaining to Atlantic salmon, however, the general inferences are relevant to a variety of taxa with complex life histories. Below we highlight major points from each area as a guide to important themes common to the entire supplement.

Within-population trends at multiple scales

Atlantic salmon provide an avenue for gaining insights into a host of pressing within-population, ecological issues (Table 2). For example, a key problem in stream fish ecology is to determine the quantitative relationship between space, food, habitat, and density, that is, productivity for territory holding fish. Atlantic salmon is ideal for these studies (Folt et al. 1998; Grant et al. 1998; Poff and Huryn 1998; Tables 1 and 2). The complex relationship between food, habitat, and density under the harsh abiotic conditions encountered by overwintering populations is another important research topic that has been well addressed by recent research on Atlantic salmon (Cunjak et al. 1998). Studies on juvenile salmon populations also offer valuable opportunities to examine how the spatial arrangement of habitat and food drive population dynamics (Kocik and Ferreri 1998), density dependence (Folt et al. 1998; Grant et al. 1998), life history decisions (Metcalfe 1998), and movements and migrations (McCormick et al. 1998).

Biotic interactions among Atlantic salmon and other species in the community have been addressed by a number of researchers and add to our understanding of context-specific processes (Tables 1 and 2). For example, studies on salmon evaluate the prevalence and impact of interspecific competition (Fausch 1998), predation (Mather 1998), biotic interactions between hosts and pathogens (Bakke and Harris 1998), and the complex set of connections between introduced and wild fish (Bakke and Harris 1998; Gross 1998; Youngson and Verspoor 1998). Furthermore, examinations of the remarkable diversity of life histories exhibited within populations of Atlantic salmon advance our general knowledge of breeding systems (Fleming 1998), migration (McCormick et al. 1998), and homing (Hansen and Quinn 1998).

One of the key points of consensus to arise from this supplement is that for Atlantic salmon, as for most species, different populations and community level processes operate at different spatial and temporal scales. Relevant spatial scales for Atlantic salmon research range from small-scale processes such as sediment dynamics to large-scale processes such as catchment geomorphology and temporal scales range from the development dynamics of individual fish through evolutionary time (Armstrong et al. 1998). Because the spatial and temporal scale influences the outcome of the research and potentially its application to management, understanding and effectively managing Atlantic salmon will be enhanced by scientific investigations that include a range of spatial and temporal scales. Human input at a variety of different levels (individual landowners; local, regional, and national government structures; international organizations such as International Council for Exploration of the Seas,

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Table 1. Conceptual organization of supplement papers.

Life history	Space, food, habitat use	Biotic interactions	Genetics	Biophysical links and anthropogenic alterations
Bakke and Harris	Cunjak et al.	Bakke and Harris	Dodson et al.	Armstrong et al.
Fleming	Folt et al.	Fausch	Fleming	Cunjak et al.
Friedland	Grant et al.	Folt et al.	Nielsen	Elliott et al.
Gross	Kocik and Ferreri	Grant et al.	Youngson and Verspoor	Parrish et al.
Hansen and Quinn	McCormick et al.	Gross		Poff and Huryn
Hutchings and Jones	Metcalfe	Mather		Wilzbach et al.
Marschall et al.	Poff and Huryn	Youngson and Verspoor		
McCormick et al.				
Metcalfe				

Table 2. How papers in this supplement contribute to improved understanding of issues related to Atlantic salmon conservation.

Within-population trends at multiple scales	Comparisons across populations	Integrating across disciplines	Incorporating the human perspective	Linking multiple ecosystems	Applied problem solving
Space, food, and habitat	Bakke and Harris	Cunjak et al.	Armstrong et al.	Friedland	Armstrong et al.
See Table 1	Elliott et al.	Kocik and Ferreri	Bakke and Harris	Hutchings and Jones	Dodson et al.
	Fausch	McCormick et al.	Dodson et al.	Mather	Fausch
Biotic interactions	Fleming	Metcalfe	Elliott et al.	McCormick et al.	Grant et al.
See Table 1	Folt et al.	Nielsen	Fleming		Gross
Life history					
See Table 1	Hansen and Quinn	Wilzbach et al.	Gross		Kocik and Ferreri
Scale					
All	Hutchings and Jones	Youngson and Verspoor	McCormick et al.		McCormick et al.
	Mather		Parrish et al.		Metcalfe
	Nielsen		Poff and Huryn		Poff and Huryn
			Wilzbach et al.		Wilzbach et al.
			Youngson and Verspoor		Youngson and Verspoor

North Atlantic Salmon Conservation Organization) will also be valuable for effective implementation of scientific advances (Armstrong et al. 1998).

In the papers that follow, these scale issues are examined in depth (Table 2) and the desirability of considering many aspects of scale while addressing applied problems is established (Armstrong et al. 1998; Dodson et al. 1998; Parrish et al. 1998; Wilzbach et al. 1998). These multiple approaches provide an array of perspectives on the choice of appropriate scale and methods for integration across scales. For example, several reviews establish the need to understand how an animal responds to spatial heterogeneity to determine the appropriate scale of an investigation. Specifically, if no heterogeneity exists, studies at different spatial scales should provide similar answers (Grant et al. 1998). Furthermore, methods for identifying heterogeneity and the appropriate scale for any sampling, research, management, or conservation plan are presented (Armstrong et al. 1998; Dodson et al. 1998). In general, the appropriate scale depends on the question being asked, heterogeneity, individual movements, and our ability to relate patterns and processes at different scales.

Because of the mismatch between scale hierarchy and process hierarchy, integrating across scales within management plans is extremely important (Armstrong et al. 1998). Working at multiple scales to identify scale inconsistencies is the first step to understanding the relationship between outcomes at large and small spatial scales (Folt et al. 1998). Addressing the same question in the same system at the same time at several spatial scales or the same question in the same system at the same spatial scale across time can reduce confounding effects. Alternate approaches such as starting at large scales and working down or extrapolating up from small, short, high-resolution studies offer benefits under different conditions. Combining components of both approaches to work simultaneously from the top down, i.e., large-scale to small-scale generalizations, and from the bottom up, i.e., small-scale to large-scale extrapolations, may provide the best information on how to effectively link large and small scales.

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Across-population comparisons

Because so many populations of Atlantic salmon exist worldwide (Parrish et al. 1998; Hutchings and Jones 1998), this species provides unique opportunities to examine across-population trends (Table 2). For example, when life history, geomorphology, and predation are compared across 275, 156, and 45 populations, respectively (Hutchings and Jones 1998; Elliott et al. 1998; Mather 1998), large-scale patterns are identified that could not be gleaned from finer grained analyses. Similarly, the relative importance of intra-and interspecific competition is a vital concern for the conservation and management of many species. Comparing 13 studies across a variety of taxa and geographic regions showed that all coevolved and non-native salmonids had interspecific effects on Atlantic salmon at least as great as intraspecific effects (Fausch 1998). The great spatial and temporal variation in Atlantic salmon life history provides a singular opportunity to compare life history variations across populations (Hutchings and Jones 1998), a methodology that complements within-population analyses (Marschall et al. 1998). Thus, a rigorous, focused hypothesis testing approach that uses individual populations as experimental units can provide information unobtainable from a descriptive approach that treats each population as unique (Mather 1998). Although comparing across populations is not desirable for all questions (Marschall et al. 1998), contrasting life history, ecological, and behavioral parameters across populations can increase the level of useful knowledge by providing synthetic trends over a wide range of environmental conditions. Moreover, these trends will be useful for other species.

Integrating across multiple disciplines

Integrating knowledge across disciplines and sharing ideas from related research areas results in innovations that can aid conservation and management. The papers that follow reveal the benefits and necessity of combining tools and approaches from diverse biological disciplines (Table 2). Specifically, synthesizing and integrating physiology, behavior, ecology, genetics, hydrology, and population dynamics in systems with Atlantic salmon provide new perspectives (Cunjak et al. 1998; Kocik and Ferreri 1998; McCormick et al. 1998; Metcalfe 1998; Nielsen 1998; Youngson and Verspoor 1998). For example, physiological readiness, fish behavior, and appropriate ecological conditions influence movements and migrations for Atlantic salmon and other species (McCormick et al. 1998). Habitat assessment, fish behavior, and population dynamics interact to influence spatially explicit habitat use (Kocik and Ferreri 1998). Further genetics, ecology, and behavior together influence local adaptation and growth trajectories of individual salmon (Metcalfe 1998; Nielsen 1998; Youngson and Verspoor 1998). In another instance, the challenges faced by salmon in winter only emerge by combining winter biology and hydrology (Cunjak et al. 1998). Taking a broader view of blending disciplines, the synthesis of biology, social science, economics, and policy can help us understand the importance of an increased human valuation of an intact ecosystem (Wilzbach et al. 1998).

However, research on Atlantic salmon has not always integrated ideas from other research areas. Specifically, in a literature review across three research areas, i.e., general ecology, fisheries biology, and Atlantic salmon biology, we compared the representation of eight research foci, (*a*) abiotic factors, (*b*) biotic processes, (*c*) competition, (*d*) predation, (*e*) integration, (*f*) synthesis, (*g*) ecosystem and (*h*) spatial and temporal scales (Fig. 2). Although the ecological and fisheries databases had a similar emphasis on abiotic factors, six times more Atlantic salmon studies addressed physical factors (Fig. 2*a*). The emphasis on biotic factors was more similar across all three research areas (Fig. 2*a*) but the ecological literature examined competition and predation more than either the fisheries or Atlantic salmon literatures (Fig. 2*a*). Little reference was made to integration and synthesis in any of the databases (Fig. 2*b*). Finally, the ecological literature emphasized ecosystem and scale the most and the Atlantic salmon literature the least (Fig. 2*b*). Although this is a quick index of which issues are addressed in three research areas, the Atlantic salmon literature appeared to be on a trajectory of its own. This volume seeks to remedy this isolation through an explicit integration and synthesis of concepts and theories identified in the general scientific literature.

Incorporating the human perspective

Many papers in this supplement frame research in a social context that directly addresses anthropogenic effects such as overfishing, introductions, dams, and habitat alterations (Table 2). For example, overfishing can adversely impact Atlantic salmon breeding success via changes in population size, maturity, size structure, sex ratio, and number and condition of breeding competitors (Fleming 1998). The introduction of fish by stocking, ranching, and aquaculture also has deleterious impacts such as the transmission of diseases and parasites from cultured to wild fish (Bakke and Harris 1998), ecological and genetical impacts (Youngson and Verspoor 1998), chemical releases (Gross 1998), and biological pollution (Gross 1998). In addition, dams are extremely detrimental to all anadromous fish and life stages because they block migration corridors (Parrish et al. 1998) and endanger the physiologically vulnerable smolt stage by delaying outmigration (McCormick et al. 1998). Furthermore, humans can negatively affect salmon via habitat fragmentation, habitat degradation, and alterations in land use (Dodson et al. 1998; Elliott et al. 1998; Kocik and Ferreri 1998; Poff and Huryn 1998; Parrish et al. 1998; Wilzbach et al. 1998). For problem solving and conservation, these deleterious human impacts must be addressed in an integrated way (Armstrong et al. 1998; Dodson et al. 1998; Parrish et al. 1998; Wilzbach et al. 1998). This volume stresses that when the keystone environmental architects, humans, are included as a part of the ecosystem, more complete and relevant management recommendations can be made and better translated into language that the public and policy makers can understand.

Linking multiple ecosystems

Explicit comparisons across habitats offer new ways of linking multiple ecosystems (Table 2). For example, in evaluating the importance of predation across extant field studies, the vulnerability of smolts in the transitional river and

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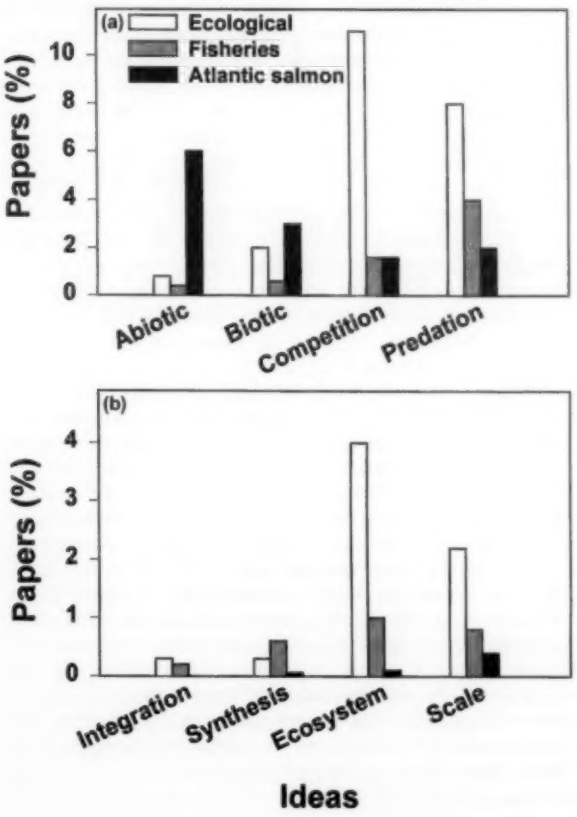
Fig. 2. Representation of eight ideas (1) abiotic factors, (2) biotic processes, (3) competition, (4) predation, (5) integration, (6) synthesis, (7) ecosystem, and (8) spatial and temporal scales in general ecology, fisheries biology, and Atlantic salmon research. The general ecology database consisted of Ecological Society of America publications, i.e., *Ecology*, *Ecological Monographs*, *Ecological Applications*. The fisheries database consisted of articles published in the *Canadian Journal of Fisheries and Aquatic Sciences* and American Fisheries Society publications, i.e., *Fisheries*, *North American Journal of Fisheries Management*, *Transactions of the American Fisheries Society*. The Atlantic salmon literature was derived from a BIOSIS database search on the keywords "Atlantic salmon." We compared these eight ideas across these three databases, and, within each database, we calculated the proportion of references related to each specific idea divided by the total number of references in that database. Thus, each bar represents the percentage of each literature database that cites each idea.



estuary habitat, relative to other areas, became clear (Mather 1998). In fact, McCormick et al. (1998) suggest that migration and movements can integrate across habitats. Questions about the relative importance of processes in the marine, freshwater, and estuarine habitats also emerge from explicit across-habitat comparisons. Although Friedland (1998) emphasizes the greater importance of marine mortality relative to freshwater mortality, Hutchings and Jones (1998) conclude that freshwater and marine mortalities were both significant for Atlantic salmon populations. In the future, explicit across-habitat tests might resolve this type of ambiguity by comparing patterns and processes in multiple habitats simultaneously using similar techniques and comparable spatial and temporal scales. Thus, these new perspectives that result from explicit across-habitat comparisons illustrate that Atlantic salmon investigations have the potential to contribute to a broader understanding of how multiple ecosystems are linked.

Applied problem solving

Many papers seek to apply research findings to specific management problems (Table 2). Specifically, recommendations are made to improve restoration and enhancement of juvenile salmon in freshwater (Grant et al. 1998; Metcalfe 1998; Poff and Huryn 1998). Several papers apply research findings to habitat management (Armstrong et al. 1998; Fausch 1998; Grant et al. 1998; Kocik and Ferreri 1998; McCormick et al. 1998). For example, failure to conserve key habitats and the capacity of fish to move between habitats are identified as critical impediments to effective management (Armstrong et al. 1998; Dodson et al. 1998; Fausch 1998; Kocik and Ferreri 1998). Recommendations for maintaining ecosystem processes that create and maintain habitats (Dodson et al. 1998) and ensure future genetic capacity (Nielsen 1998; Youngson and Verspoor 1998) have relevance for effective conservation of salmon and other species. Finally, several authors make specific socioeconomic and policy suggestions (Dodson et al. 1998; Gross 1998; Wilzbach et al. 1998) such as a plea for scientists to take a more active role in the implementation of science-based management (Armstrong et al. 1998). Thus studies of Atlantic salmon and papers in this volume provide examples of how research can address applied conservation and management problems.

Future research

Standardized data

Although each paper makes specific recommendations for future research, common information gaps are identified. First, many authors identify the value of standardized archives. An inventory of Atlantic salmon rivers, identification of keystone habitats, and documentation of the present and historical status of salmon populations would provide useful information for future conservation plans (Dodson et al. 1998). Also beneficial would be time series data on important life history parameters from individual systems (>10 years; Marschall et al. 1998), greater documentation of genetic diversity within and across populations (Youngson and Verspoor 1998), standardized data on the intensity of predation and concurrent abiotic and biotic conditions across systems and years (Mather 1998), and a better map of Atlantic salmon distributions at sea (Hansen and Quinn 1998). Hutchings and Jones (1998) counsel the establishment of a web site to quantify life history parameters of Atlantic salmon worldwide, a suggestion that could be expanded to establish an on-line repository for all physical and biological data on this taxa.

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Ecological research

A number of authors identify ecological research questions. For example, when and where do bottlenecks occur in different systems (Armstrong et al. 1998), what abiotic and biotic factors influence salmon (Wilzbach et al. 1998), how do numbers and production of juvenile salmon relate to food availability (Folt et al. 1998), how does variation in production affect growth opportunity (Metcalfe 1998), can salmonid abundance be altered by manipulating territory size (Grant et al. 1998), and how does density dependence influence growth and juvenile survival (Kocik and Ferreri 1998; Metcalfe 1998)? In addition, the role of complex interactions and context-specific processes, i.e., interactions that change with altered environmental conditions, require further clarification (Cunjak et al. 1998; Fausch 1998; Mather 1998). More information about the effects of aquacultured Atlantic salmon on wild fish in both the Atlantic and Pacific is needed (Gross 1998), especially related to the pathogens that affect wild salmon (Bakke and Harris 1998). Gaps in our knowledge also exist relative to how the spatial arrangement of habitats affect juvenile growth and survival (Folt et al. 1998; Kocik and Ferreri 1998) and the role of parr movement in linking these freshwater habitats (Fausch 1998; Kocik and Ferreri 1998; McCormick et al. 1998).

Scale issues

A number of exciting topics related to scale emerged. Because most Atlantic salmon research, as reviewed here, concentrates on small, short, high-resolution scales, research at broad spatial and temporal scales that better match those of the salmon is warranted (Armstrong et al. 1998; Folt et al. 1998; Wilzbach et al. 1998). However, individual based examinations of mechanisms underlying biotic processes remain essential to clarify large-scale field patterns (Mather 1998). Second, because our traditional focus has been on local habitats (Poff and Huryn 1998), in the future, research at multiple levels can identify scale inconsistencies (Folt et al. 1998). Finally, techniques for the extrapolation of processes are needed for the development of general rules to predict the management requirements of stream systems (Armstrong et al. 1998).

More effective methods

Many papers make methodological suggestions. Relative to existing methods, better use of known principles of experimental design, i.e., controls, adequate replication, environmental conditions that mimic nature as much as possible, and a design that does not confound intra- and interspecific effects, is advocated (Fausch 1998). Furthermore, combining observations with manipulative approaches to elucidate mechanisms and using quantitative, across-study comparisons such as meta-analyses can increase methodological rigor and the generality of results (Folt et al. 1998; Mather 1998). Benefits also can be gained by adopting tools from other disciplines. For example, the paradigms of landscape ecology can enhance our understanding of habitat fragmentation, heterogeneity, connectivity (Armstrong et al. 1998; Kocik and Ferreri 1998). A spatially explicit approach can help us better understand food, space, and habitat use (Folt et al. 1998; Kocik and Ferreri 1998). Finally, the use of coherence patterns may help explain variability in marine mortality (Friedland 1998).

More intricate models may also provide important information (Folt et al. 1998; Marschall et al. 1998; Metcalfe 1998; Wilzbach et al. 1998). For example, models that synthesize within-population trajectories and identify correlations among individual life history traits will be useful for predicting how changes at one life stage translate into changes at another (Marschall et al. 1998). Mechanistic models that incorporate physiological and behavioral mechanisms underlying life history variation can help discern environmental impacts on life history parameters (Metcalfe 1998). Interdisciplinary models can enhance our understanding of how human systems and Atlantic salmon ecosystems interact (Wilzbach et al. 1998).

Genetics

Because the growth in our knowledge of biochemical processes is paralleled by how little we know about underlying processes of evolution and genetic mechanisms, numerous genetics problems remain to be investigated (Nielsen 1998). For example, the demographic and genetic consequences for life history traits like male parr maturity (Hutchings and Jones 1998), the role of quantitative genetics and phenotypic plasticity (Hutchings and Jones 1998; Marschall et al.1998), the genetic status of wild fish (Youngson and Verspoor 1998), and heterogeneity and performance prior to selection at early life stages (Metcalfe 1998) merit further investigation. When more is known about these issues, we will be better able to define and conserve evolutionarily significant units (Nielsen 1998; Youngson and Verspoor 1998).

Linkages

Advances will also occur as relationships between environmental conditions and salmonid biology are quantified. Links among environmental harshness, habitat use, and juvenile survival identified with experiments that test interactions among physiology, life history, behavior, and ecology can provide insights in this area (Cunjak et al. 1998). Better region and year-specific correlations among distribution, growth, survival, climate, temperature, current, and available prey will also augment our understanding of variability in Atlantic salmon abundance (Hansen and Quinn 1998). Furthermore, identification of connections between genetics and known adaptive changes (Nielsen 1998; Youngson and Verspoor 1998) and elucidation of links between stock specific physiological, life history, behavioral parameters and characteristics of home rivers is needed (McCormick et al. 1998). These data can then be integrated into a biophysical template (Elliott et al. 1998).

Management

Classification schemes that categorize similar systems would allow management actions to be generalized across systems (Armstrong et al. 1998). Biosocial research will also increase the efficacy of management (Dodson et al. 1998; Gross 1998; Wilzbach et al. 1998). In particular, understanding what kinds of institutions, regulations, and policies lead to effective conservation and management and how changes in feedback mechanisms influence human valuation of the resource is critical (Wilzbach et al. 1998). Finally, to address

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all of these research areas, the formation of an Atlantic salmon forum, an international research organization that considers environmental and management issues pertaining to salmon in a multi-species research arena, is advocated (Wilzbach et al. 1998).

Conclusions

A growing human population does not spell inevitable doom for Atlantic salmon and other species if we combine sound science with an understanding of human interactions to promote conservation-oriented development (Wilzbach et al. 1998). Specifically, the papers in this supplement provide new ways to examine within-population ecological trends, understand multiple scales, integrate across disciplines, incorporate the human perspective, link multiple ecosystems via across-habitat comparisons, and apply science to complex natural resource problems. Hopefully, this volume can provide guidance for the broader disciplines of fisheries biology, ecology, and conservation biology. With increased rigor and synthesis, our understanding of patterns and processes in larger ecosystems can help sustain species like Atlantic salmon.

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Implications of temporal and spatial scale for Atlantic salmon (*Salmo salar*) research

Carol L. Folt, Keith H. Nislow, and Mary E. Power

Abstract: The Atlantic salmon (*Salmo salar*) is a model species for studying scale issues (i.e., the extent, duration, and resolution of a study or natural process) in ecology. Major shifts in behavior and habitat use over ontogeny, along with a relatively long life span and large dispersal and migration distances, make scale issues critical for effective conservation, management, and restoration of this species. The scale over which a process occurs must be linked to the research design and we illustrate this with a discussion of resource tracking by Atlantic salmon. Identifying scale inconsistencies (e.g., when a process is evident at one scale but not another) is shown to be an effective means by which some scale-dependent processes are understood. We review the literature to assess the temporal and spatial scales used in Atlantic salmon research and find most current studies appear to sacrifice spatial and temporal extent for increased resolution. Finally, we discuss research strategies for expanding the temporal and spatial scales in salmon research, such as conducting multiple scales studies to elucidate scale inconsistencies, identifying mechanisms, and using techniques and approaches to generalize across studies and over time and space.

Résumé : Le saumon de l'atlantique (*Salmo salar*) est une espèce modèle pour l'étude des problèmes d'échelle (c'est-à-dire l'étendue, la durée et la résolution d'une étude ou d'un processus naturel) en écologie. Les changements majeurs dans le comportement et l'utilisation de l'habitat durant la vie du saumon atlantique, ainsi que la longévité relativement grande et l'importance de la dispersion et de la migration de ce poisson, rendent critiques les problèmes d'échelle pour la conservation, la gestion et le rétablissement de cette espèce. L'échelle sur laquelle se déroule un processus doit liée au protocole de recherche, et nous examinons cette question en rapport avec la recherche de ressources par le saumon atlantique. On montre que le repérage du manque de cohérence entre les échelles (p.ex., quand un processus est évident à une échelle donnée mais pas à une autre) est un moyen pour comprendre les processus dépendants de l'échelle. Nous avons examiné la documentation scientifique pour évaluer les échelles temporelles et spatiales utilisées dans la recherche sur le saumon atlantique et avons trouvé que la plupart des études actuelles semblent étendues spatiales et temporelles pour obtenir une plus grande résolution. Enfin, nous traitons des stratégies de recherche permettant d'étendre les échelles temporelles et spatiales dans la recherche sur le saumon; on propose notamment d'effectuer des études à échelles multiples pour élucider les incohérences d'échelle, de repérer les mécanismes, et d'utiliser des techniques et des permettant de faire des généralisations à partir des diverses études et dans le temps et l'espace.

[Traduit par la Rédaction]

Introduction

Ecologists increasingly recognize the importance of scale (i.e., the extent, duration, and resolution of studies and natural processes) to many issues, including salmonid ecology, conservation, and restoration. Because different biotic and abiotic processes act at different spatial and temporal scales, the conclusions of research studies often are influenced by the scale of investigation (Allen and Hoekstra 1992; Levin 1992; Fahrig 1992; Ray and Hastings 1996). Interest in the effect of scale on diverse topics can be seen from the number of recent reviews addressing scale in aquatic habitats. These reviews have considered the importance of scale to questions such as the design and interpretation of research (Frost et al. 1988), fish habitat conservation and restoration programs (Lewis et al. 1996), and the effect of environmental constraints on species distributions and abundances (Poff 1997)

The Atlantic salmon (*Salmo salar)* is a good model species for evaluating the importance of scale because processes affecting its growth, reproduction, survival, and evolution span a wide range of temporal and spatial scales. Atlantic salmon undergo major ontogenetic shifts in behavior and habitat use (Mills 1991), are relatively long-lived (2–10 years), occupy a broad geographical range (circum North-Atlantic from southern New England to the Iberian peninsula) and disperse and migrate over extremely long distances (up to 1000s of kilometres).

As a result of these processes, a number of important questions about Atlantic salmon cannot be adequately addressed without taking temporal or spatial scale into consideration. For example, effects of logging on salmonid habitat clearly vary over different spatial and temporal scales (e.g., are scale dependent). Consider the temporal and spatial scales of impact resulting from clear-cutting the forest along a 500 m stream reach. Effects of increased light penetration on instream temperature and primary productivity due to

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C.L. Folt and K.H. Nislow. Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, U.S.A.
M.E. Power. Department of Integrative Biology, University of California at Berkeley, Berkeley, CA 94720, U.S.A.

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canopy opening are likely to be evident at relatively limited temporal (in the year following logging) and spatial (~500 m) scales (Hicks et al. 1991). In contrast, effects of the clear-cut on stream sediment load, channel morphology, and large woody debris loading are likely to extend beyond the stream reach where logging has occurred (larger spatial scale) and not be fully manifest until years following the logging event (larger temporal scale). Moreover, effects at the large scale can also feed back over longer time periods to influence small-scale food web processes through their influences on life cycles and interactions among species (Power et al. 1996; Wootton et al. 1996). Despite its recognized importance, few studies of Atlantic salmon have specifically included more than one scale in their design.

To understand fundamental processes underlying Atlantic salmon ecology requires linking physical and biological processes at appropriate temporal and spatial scales. In this review, we address scale-dependent processes that can affect the dynamics of salmon and other fish species. This paper is an overview, using a few key examples to illustrate how scale can affect the interpretation of pattern and process. We review the literature to assess the scales of investigation most frequently used in Atlantic salmon research and discuss how scale can affect research conclusions. Finally, we emphasize the benefits of combining observations with experimental and manipulative approaches for elucidating mechanisms and identifying appropriate scales in the study of Atlantic salmon.

What is scale?

"Scale" is the spatial and temporal dimension of a process or an entity (Lewis et al. 1996). For example, habitat selection by salmon is a *process* whereby individuals make certain "decisions" based on information they have integrated over particular distances and times. The size of a study area and the duration of a study are attributes of an *entity* (the research study) whose characteristics are in part defined by these dimensions (e.g., diversity may increase with plot size up to a certain point; more behaviors are observed as observation period increases).

Allen and Hoekstra (1992) define three dimensions of scale: (1) spatial extent (the size of a process or entity), (2) temporal extent (the duration of a process or entity), and (3) grain (the finest level of spatial and temporal resolution, often determined by the frequency and density of samples or observations, or by levels of data aggregation). For example, Elliott's (1994) long-term study of brown trout population dynamics at Black Brow's Beck is of small spatial extent (conducted in a single stream reach of approximately 60 m^2), large temporal extent (stretching more than 20 years, encompassing multiple generations), and fine-grained (the population was sampled multiple times each year).

Extent and grain tend to be related in study design. Fine-grained (high-resolution) studies generally are performed over limited spatial and temporal scales. The terms "small-scale" tend to refer to processes or entities that are small in extent and (or) relatively fine-grained, and "large-scale" for processes or entities that are large in extent and (or) relatively coarse-grained. Given finite research resources, increased resolution (fine grain) is generally achieved by reducing the spatial or temporal extent of the study, or vice versa.

We illustrate these aspects of scale with three hypothetical studies of salmon summer growth rates and show that the questions that can be adequately addressed differ among the designs due to differences in extent and grain. First, in a single stream, growth is measured only once at the end of the season, for 10 consecutive years (small spatial extent, large temporal extent, coarse-grained). This study could be used to examine the influence of between-year variation in climate and discharge on growth of a single population. Second, also in a single stream, growth is measured at 10 intervals over a single growing season (small spatial extent, small temporal extent, fine-grained). This study could be used to examine the importance of short-term critical growth periods, but only for one population (among basin comparisons could not be made). Third, in 10 different streams, growth is measured once at the end of a single growing season (large spatial extent, small temporal extent, coarse-grained). This study could be used to address effects of stream-scale differences in geomorphology and water chemistry on annual first-year growth, but not within season patterns of growth within a site or the importance of yearly variation. Extending the extent or grain can reveal potentially important processes that operate at different scales.

Review of the Atlantic salmon literature reveals cases where information gathered at a particular scale is broadly applied without considering implications of the scale of the original sampling design (i.e., when inferences drawn from a single site are assumed to apply over broader spatial or temporal extent). To avoid this problem, careful attention must be given to the scale over which a process occurs and is measured and over which it influences a specific aspect of salmon biology. Fahrig (1992) states this succinctly. "To understand the relationship of an organism to its environment, one must understand the interactions between the intrinsic scales of heterogeneity within the environment and the scales at which the organism can respond to this heterogeneity." In Table 1, we list three environmental factors (current speed, temperature, and prey abundance) that are known to have a strong influence on spring/summer juvenile salmonid growth and survival and are highly variable in streams (Bjornn and Reiser 1991). These processes are driven by different factors at different spatial scales (Table 1). For example, stream flow at small spatial scales (within in pool or riffle) is strongly affected by local substratum characteristics. Over the entire basin, stream flow (i.e., discharge) is influenced by the geology, slope, regional land use, and precipitation.

Similarly, the effects of temperature and prey abundance on salmon growth patterns can vary at different scales. Temperature, for example, may vary only slightly at a small spatial scale and hence produce no variation in growth rate among fish within a pool, riffle, or stream reach. Nevertheless, temperature variation across basins may be great and drive large among-basin variation in salmon growth, physiology, and production (Elliott 1985; Holtby 1988; Nicieza et al. 1994; Filbert and Hawkins 1995). In seeking to understand growth patterns small-scale studies might obscure the overriding influence of temperature, even if temperature across a region was the single most important explanatory

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Table 1. Environmental determinants of three factors (current speed, temperature, and prey abundance) influencing spring/summer parr production at different spatial scales (from review by Bjornn and Reiser 1991).

Scale	Current speed	Temperature	Prey abundance
cm–m	Local substratum characteristics and small-scale channel geometry (width/depth)	Little influence at this scale	Availability of appropriate habitat patches (i.e., where are the patches of high invertebrate abundance?) Local current speeds (i.e., influences prey delivery rates and foraging success)
m – 100 m	Channel slope, sinuosity, macrohabitat transitions (riffle to pool)	Ground water sources	Larger scale habitat units (riffles runs) Shading effects on primary production
100 m – km	Land use, impoundment	Overhead cover, shading, impoundment	Downstream dispersal Temperature effects on invertebrate production Allochtonous inputs
km – 100 km	Basin size, parent geology	Basin-wide influences on runoff and temperature	Basin chemistry and geology
>100 km	Regional precipitation and runoff	Regional climate	Regional species pool

variable. Prey abundance also may vary less over small spatial scales than large scales. As for temperature, it could be difficult to isolate the influence of food abundance on salmon production even from numerous small-scale or high-resolution studies.

Important processes also have influence at different temporal scales (Table 2). For example, size related shifts in habitat and diet of Atlantic salmon may be explained in part by seasonal shifts in prey phenology and stream discharge that occur over periods of weeks to months (Cada et al. 1987; Keeley and Grant 1997). Over the short term, we may expect the most productive reaches to be those with the most food and the best discharge conditions. Yet, over the long term, overall patterns of fish or prey abundance may be driven by infrequent extreme events (e.g., massive discharges or dry periods) that are regulated by climate trends operating over years to decades and beyond. These long-term processes may result in low population numbers persisting in reaches that in any given year (or in a short-term study) appear to provide highly suitable habitat.

In the next section, we illustrate the importance of scale by examining the relationship between stream dwelling salmon and their food resources. We then discuss inferences that can be made by looking at this question over different spatial and temporal scales and with different resolution.

Resource tracking and the importance of scale

It is common in fisheries science to predict fish production from the quantity of resources (e.g., food, physical habitat type) in an area. The term "resource tracking" has been used to describe situations where there is a significant positive correlation between the abundance or performance of consumers and the abundance or productivity of their resources (Hart and Fonseca 1995). If resource tracking occurs, the resource levels can be used for goals such as identifying habitats likely to yield high fish production, evaluating the efficacy of habitat remediation, and understanding how fish production will respond to variation in resource abundance.

Much effort has been directed towards testing whether salmon abundance (density, standing stock biomass, production) and performance (growth, survival, reproduction) track the abundance of resources such as prey (Mason 1976; Cada et al. 1987; Hinch 1991; Richardson 1993; Filbert and Hawkins 1995) or habitat (Fausch et al. 1988; Hicks et al. 1991; Fausch et al. 1994). These studies have been conducted over a range of spatial and temporal scales and illustrate how scale affects the examination of an important ecological process. We use studies from various systems relevant to and including Atlantic salmon to show that (1) different types of resource tracking require different measurements, (2) resource tracking may be measurable over one spatial scale but not another (we term this "scale inconsistency"), and (3) understanding the mechanism underlying the resource tracking relationship or scale inconsistency helps identify the appropriate measurement scale.

Types of resource tracking

Fish production tracks resources in two, non-mutually exclusive ways. Understanding their differences is necessary to interpret patterns and to predict the extent and resolution necessary to detect resource tracking in nature. We term the first type, "numerical resource tracking" (NRT), which occurs when more individuals are found at the highest resource productivity. NRT arises from an increase in recruitment or by immigration into high resource areas. We term the second

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Table 2. Temporal scale of important environmental processes and implications for Atlantic salmon (from review by Bjornn and Reiser 1991; Hicks et al. 1991).

Scale	Environmental patterns and processes	Effects on salmon
Hour–weeks	Diel cycles in oxygen temperature	Hypoxia for alevins and incubating eggs
	Diel cycles in prey availability (i.e., drift periodicity	Diel feeding and activity cycles of fry and parr
	Small-scale (aseasonal) stream discharge and temperature changes	
Weeks–year	Prey phenology	Size-related habitat and diet shifts affects feeding and growth for fry and parr
	Seasonality in temperature and discharge at high latitudes	Seasonal habitat and behavioral shifts and summer/winter habitat shifts for parr
		Migration cues/physiological changes for parr-smolts
		Redd de-watering and scouring (eggs/alevins)
Years–decades	Between-year climatic variability (ENSO, oceanic processes)	Oceanic prey availability and temperatures affecting growth and survival of adults
		Variation in precipitation and streamflow associated with ENSO, ocean circulation events (all freshwater life stages)
>Decades	Climate change, adaptation and changes in migration patterns, fishing pressure, land use change	Changes in the timing, magnitude and variability of extreme events
		Changes in stream habitat morphology (LWD availability and dynamics) sediment/substratum characteristics, channel characteristics

type, "performance resource tracking" (PRT), which occurs when individual performance (but not necessarily density) increases with resource productivity. When both NRT and PRT occur more individuals with greater individual performance are observed under high resources.

If populations are dense, so that resources have become limiting, numerical resource tracking can preclude performance tracking (PRT) and vice versa. For example, under the "ideal-free distribution" model (IFD, sensu Fretwell and Lucas 1970), individuals fill habitats sequentially, filling the best habitats first, and occupying the second best habitat when crowding lowers the quality of the first habitat to that of the second. The outcome of this ideal free distribution is that abundance tracks habitat quality, but individual performance is similar across habitats. Algivorous catfishes in tropical streams provide an example of the IFD model in situ (Oksanen et al. 1995). Non-territorial catfish in a Panamanian river showed evidence of NRT because there were more catfish in stream pools with higher algal productivity. However, there was no evidence for PRT, in that fish from high and low productivity pools exhibited similar individual growth and survival rates (Power 1984).

Distinguishing between NRT and PRT has management implications. First, different measurements over different spatial and temporal scales are required to detect each process. For example, testing for a correlation between abundance and habitat characteristics, probably the most basic and often used metric in salmon habitat studies (Bovee 1986; Fausch et al. 1988), will not yield evidence of resource tracking if only PRT occurs. Similarly, measures of individual performance do not correlate with resource abundance under an IFD/NRT-only situation. In either case, it could be erroneously assumed that a particular resource was not limiting. Second, the management of a particular system may depend on whether the performance (bigger or more fecund fish) or the abundance (more individuals) is the outcome to be maximized. Understanding the mechanistic link between resources and their specific effects on growth or abundance could be effective for improving assessment and management.

Surprisingly, there is not a clear answer in the literature as to what happens to salmon production when food resources are increased. Do you get more small fish (NRT), few big fish (PRT), more big fish (NRT and PRT), or no change at all? There are plausible models to explain any of these outcomes, but few direct tests. The relationship between food resources and NRT or PRT for Atlantic salmon can be difficult to detect and therefore easy to ignore for several reasons. First, food resource abundance and productivity can be extremely hard to quantify (Resh and Rosenberg 1979). Second, salmon may respond to an increase in resources in ways that result in either NRT or PRT. For example, territory size of individual salmon may decrease with an increase in prey flux. NRT could then arise by packing in more territories at high resources. If, as in the IFD model, territory size declines in direct proportion to an increase in food density, consumption rates remain equal across territories, and there is no PRT. In contrast, salmon territory size may not decrease with food resource density, if, for example, it has a fixed relationship with body size. Then more territories will not "pack in" at high resource levels, and NRT should not be observed. If consumption rates still increase with increasing food resources, there will be PRT without NRT.

The literature includes studies that partially support and reject NRT and PRT for salmonid systems. Elliott (1994) measured an increase in individual growth rates with an

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increase in food resources, providing strong evidence for PRT by brown trout in Black Brow's Beck. His study also provided evidence against an IFD/NRT situation, because territory size did not decline with an increase in resources. In contrast, both Dill et al. (juvenile coho, 1981) and Keeley and Grant (Atlantic salmon, 1995) found mild support for territory size compression at higher food, and thus indirect support for NRT and aspects of the IFD model. However, the effect of food on territory size was very small, explaining ~2% of the variance in territory size for Atlantic salmon parr (2.90–14.50 cm fork length; Keeley and Grant 1995). Instead, body size was a much stronger determinant of territory size. Direct tests of both NRT and PRT are needed to assess their relative importance as mechanisms linking food and production. Increasing consistency in the methods for assessing food and territory size will expand our general understanding of this issue.

Scale inconsistencies

Consideration of the extent and resolution of each study is critically important for interpreting the relationship between salmonids and their resources. If either salmon abundance or performance tracks resources at one scale but not another, studies at different scales will arrive at different answers (i.e., there will be scale inconsistencies). Scale inconsistencies present another layer of complexity in testing for resource tracking. Mason (1976) provides a good example where identifying scale inconsistencies can reveal important processes. In a stream fertilization experiment run over a period of several months (small temporal extent), juvenile coho salmon survival and growth strongly increased with increased prey productivity (NRT and PRT). Yet, when followed for several years (greater temporal extent), all evidence of NRT or PRT was absent, because they were apparently offset by heavy winter mortality. The evidence for NRT and PRT depended on the temporal scale or extent of the study, and examination of both temporal scales was necessary to fully assess the relative importance of food, performance, and a third key variable, winter survival.

Additional examples from both riverine and marine environments also show that fish track resources at some scales, but not others. Rose and Leggett (1990) found that the correlation between the abundance of Atlantic cod and its major prey, capelin, in the North Atlantic (NRT) differed strongly over different spatial scales. At the largest spatial scale measured (4–10 km), predator abundance was strongly positively correlated with prey abundance, and both species were concentrated in large-scale oceanic fronts. However, at smaller spatial scales (2–3.5 km) prey and predator abundance were either negatively correlated or uncorrelated. They interpreted this scale inconsistency as evidence for either small-scale predator avoidance by capelin or small-scale prey depletion by cod. The importance of scale inconsistencies, in this and other examples, is often that they provide the strongest tool for assessing the scale over which different processes operate.

In riverine habitats, Fausch et al. (1994) also found scale inconsistencies in the relationship between abundance of two species of char (genus *Salvelinus*) with physical and biotic factors on Hokkaido Island, Japan. Char abundance correlated positively with certain physical characteristics at large and intermediate spatial scales (e.g., watersheds and tributaries within watersheds), but was uncorrelated with these features at smaller spatial scales (e.g., within tributaries or stream reaches). In contrast, the presence of the congeneric species did not influence species' presence or abundance at larger spatial scales, but correlated with abundance at small spatial scales. By comparing processes at several spatial scales, the scale inconsistencies could be identified, and the mechanisms underlying them could be elucidated.

Elucidating mechanisms to resolve scale inconsistencies

We and others (Hart and Fonseca 1995; Lewis et al. 1996; Power et al. 1998) recommend a two-part approach to identify and then resolve scale inconsistencies. This approach combines taking explicit measurements or observations at several scales and using experiments or models to test mechanisms underlying the patterns and to probe inconsistencies that are revealed. Moreover, as Power et al. (1998) argue, if the spatial scale addressed increases (e.g., from microhabitats to watersheds), carefully designed field measurements and direct observations become even more important because large-scale manipulations are difficult to carry out and virtually impossible to replicate. They suggest that nesting experiments or models within observational field studies is most effective for clarifying mechanisms and extrapolating across systems or scales.

We illustrate the strength of this combined approach for studying resource tracking with Power's study of algivorous catfish in large tropical rivers (Power 1984; Oksanen et al. 1995; see also Power et al. 1998 for additional examples). Resource tracking was explicitly compared at two spatial scales. Power found NRT at the relatively large spatial scale (between river pools), but no evidence for NRT at the smaller scale (within pools). Catfish were more abundant in deep microhabitats farther from the riverbank, while algal standing crops were higher in shallow, nearshore sites. The mechanism underlying the inconsistency was elucidated in predator exclusion experiments. Catfish were found to avoid nearshore habitats to reduce predation risk from wading birds, who could not forage effectively in the deeper, offshore water (Power et al. 1989). In contrast, catfish resource tracking was not constrained by predation at the between-pool scale because they spent relatively little time in shallow intervening riffles when moving between pools.

Our second example involves resource tracking by age-0 Atlantic salmon. In a study of prey availability and foraging by Atlantic salmon parr in several New England streams, Nislow et al. (1998) assessed PRT at two spatial scales. They compared salmon foraging rates (by watching fish via snorkeling) as a function of potential food availability (1) among salmon occupying different feeding locations within a reach (small scale) and (2) among salmon living in different streams. Within each stream, territory-specific drift rates were predicted as the mean free stream velocity in each territory times the mean drift concentration within the reach. Between streams, mean foraging rates tracked food resources (PRT). Foraging rates were significantly reduced by experimental reduction of the mean density of drifting prey

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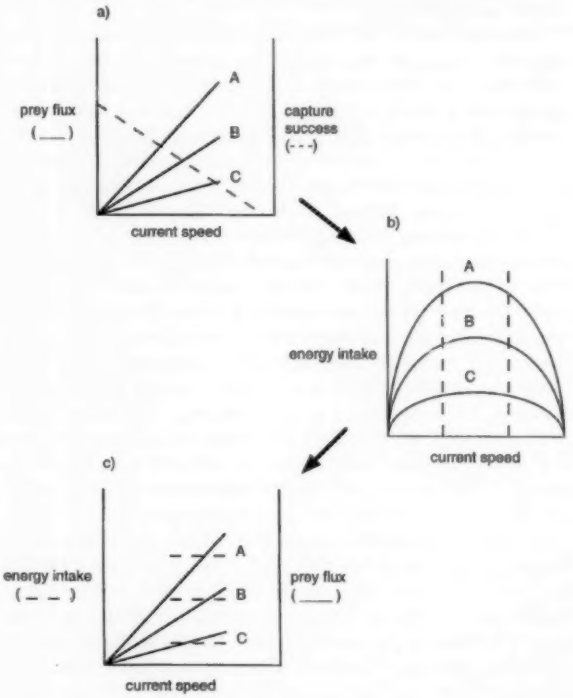
to the reach and were higher in the high-food stream. In contrast, at the small scale (comparing among fish within a reach), there was no PRT (i.e., there were not higher foraging rates in high-current-speed, high-food locations (territories) within each stream). These results indicate a scale inconsistency in resource tracking by age-0 salmon.

One explanation for this scale inconsistency derives from understanding the mechanisms relating current speed, food flux, capture success, and microhabitat selection by stream salmonids. Among microhabitats within a stream reach, invertebrate drift rates tend to be strongly positively correlated with microhabitat current speed (Waters 1972; Bjornn and Chapman 1968; Hill and Grossman 1993; Nislow et al. 1998). However, high current speeds also decrease the ability of fish to detect and capture drifting prey. Because of this tradeoff, consumption rates are predicted to be maximized at intermediate current speeds (and thus at intermediate prey flux rates), and juvenile salmonids are predicted to preferentially occupy those microhabitats where consumption is predicted to be maximized (Hughes and Dill 1990; Hill and Grossman 1993).

Some stream salmonids, including Atlantic salmon, appear to select habitats in accordance with tradeoffs predicted by this model (Hughes and Dill 1990; Hill and Grossman 1993; Nislow et al. 1999). Under these model conditions, it is unlikely that performance (as foraging rate) tracks food resource abundance at the within-reach scale (Fig. 1), for two reasons. First, optimal current velocities (i.e., the velocities predicted to produce within ±10% of the highest feeding rates based on tradeoffs between capture success and prey flux with current speed) can span a fairly wide range (i.e., roughly the same feeding rates are predicted to result over a range of current velocities). Second, because capture success declines with current speed and prey drift rate increases with current speed, high prey drift rate is not the same as high resource availability. Therefore, food abundance alone is not a proper currency for assessing food availability, and feeding will not necessarily track food abundance. Like the catfishes studied by Power (1984), salmon do not track their food on some scales, due to the positive correlation between resource abundance and factors that impede resource use (predation risk in the case of the catfishes; reduced capture success at high current speed in the case of salmonids).

In contrast, differences in resource abundance between salmon rearing streams are correlated with differences in performance (Nislow et al. 1998). In fact, any constraint at the within-reach scale that reduces within-reach variation in foraging may make it easier to detect differences between high and low resource reaches, and reinforce PRT at the larger spatial scale. This example therefore illustrates both how understanding mechanisms can help resolve "scale inconsistencies," and how processes that occur on small scales can influence processes at larger scales of observation. Lewis et al. (1996) provide other examples where multiscale investigations were effective for determining the appropriate scale for restoration and management practices such as liming to increase pH (Lacroix 1996; Keller and Gunn 1995 in Lewis et al. 1996) or habitat management (Crowder et al. 1996).

Fig. 1. Diagrammatic representation of resource tracking at the between-microhabitat vs. between-reach scales for juvenile Atlantic salmon. Figure 1*a* describes the relationship between current speed, prey flux (prey/time), and capture success (% of prey successfully captured) in three hypothetical stream reaches of different mean prey densities (prey density = slope of the current speed prey flux relationship; reaches labeled A-C in descending order of mean/prey density). Figure 1*b* shows the corresponding relationship between energy intake (prey flux · % capture success) vs. current speed in the three reaches. Dashed vertical lines define the range of current speeds (predicted to yield within 10% of maximum energy intake rates) predicted to be occupied by salmon. Figure 1*c* shows that consumption is predicted to track differences in prey between reaches (A > B > C), but not to track differences in prey flux as a function of local current speed within reaches (no significant linear relationships (indicated with dashed lines in the diagram) between current speed and energy intake within each reach).



Over which scales are most studies conducted?

The need to consider temporal and spatial scale to address important issues for Atlantic salmon ecology is becoming widely appreciated. This volume includes a number of papers that deal explicitly with scale issues at the physiological, population and community level, and in freshwater and oceanic phases. Major shifts in behavior and habitat use over ontogeny, along with a relatively long life span and large dispersal and migration distances, make scale issues critical for effective conservation, management, and restoration of

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Atlantic salmon. Nevertheless, relatively few studies have been conducted at more than one spatial or temporal scale, resolution varies across studies, and experimental field studies to tease apart mechanisms are still uncommon.

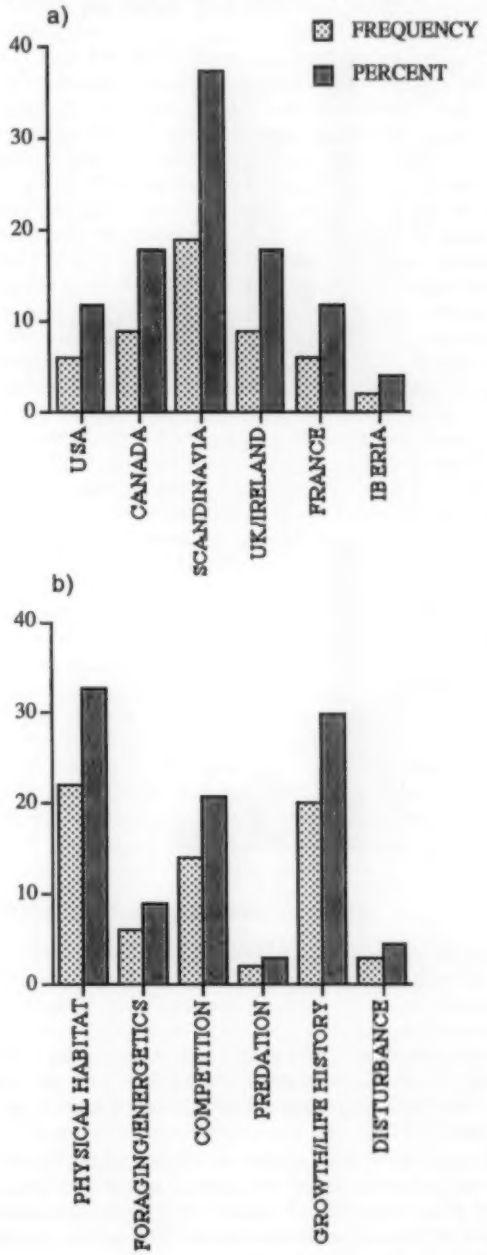
To determine the spatial and temporal scales over which most Atlantic salmon studies have been conducted, we ran an on-line computer search. We considered two components of scale: (1) extent — the number of years or streams in a study and (2) grain — the number of samples/year or sites/stream in a study. We used the on-line search engine (Ovid: Gateway) to search the major life sciences database (BIOSIS for the Life Sciences) for all citation abstracts containing the key words "Atlantic salmon" and "ecology" from 1990 through February 1997. Of these citations, we included only papers which assessed, using field manipulation, correlations or comparisons, factors affecting habitat selection, life-history strategies, growth, and survival of freshwater-phase anadromous Atlantic salmon. Laboratory and aquaculture studies were excluded.

Studies were classified by both spatial and temporal extent and resolution. We distinguished four levels of temporal extent, equivalent to study duration: ≤1 year, 2–5 years, 6–10 years, and >10 years. We distinguished two levels of temporal grain or resolution, equivalent to the within-year sampling frequency: one sampling period a year (coarse grain) or multiple sampling periods a year (fine grain). For spatial extent, we distinguished four categories: studies which took place within 1 stream or river, 2–5 rivers, 6–10 rivers, and greater than 10 rivers. For spatial grain, we classified studies on the basis of whether they sampled one site/river (coarse grain) or multiple sites/river (fine grain).

It was more difficult to classify the spatial scale of each study than the temporal scale. Depending on the design and objective of the study, studies conducted in multiple tributaries of the same river system can be considered as multiple rivers in our classification system or as multiple sites within a single drainage system. For example, if multiple tributaries of a single river were sampled, we classified this study as being conducted in more than one tributary or stream (i.e., increased spatial extent) if the aim of the study was to compare some factor among streams (grain depends on whether there were replicate sites sampled). However, if the study was conducted in multiple tributaries of a single river, and the object was to use the average of these sites to obtain a average for that single drainage system, then we classified the study as characterizing a single river system, but with finer grain (e.g., more replicates).

To illustrate our classification scheme, consider McMenemy's (1995) study of the effect of stocking density on juvenile Atlantic salmon survival in the West River, Vermont, U.S.A., over 7 years. Sampling sites were distributed among different tributaries of the West River, and were censused once each year. The study tested the effects of variation in stocking density across years averaged across tributaries and did not address between-tributary differences. Therefore, we considered the spatial extent of this study to be a one river system (the West River), and the spatial grain to be multiple sites/river (fine grain). The temporal extent is 6–10 years, and the temporal grain is one sample/year (coarse grain).

Fig. 2. Distribution of Atlantic salmon studies (1990–1997) uncovered by literature search over geographic locations (Fig. 2*a*) and general research topics (Fig. 2*b*). Additional details on literature search given in text. $N = 51$ studies, some studies were placed in more than one research topic category.



We identified 51 field studies that fulfilled our selection criteria. Of these we were able to determine spatial extent of 50 studies, temporal extent of 41 studies, temporal grain of 32 studies, and spatial grain of 33 studies. These studies

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Fig. 3. Frequency and percentage of Atlantic salmon studies conducted at 5 categories of temporal (Fig. 3*a*) and spatial (Fig. 3*b*) extent. Details of the literature search and classification criteria given in text.

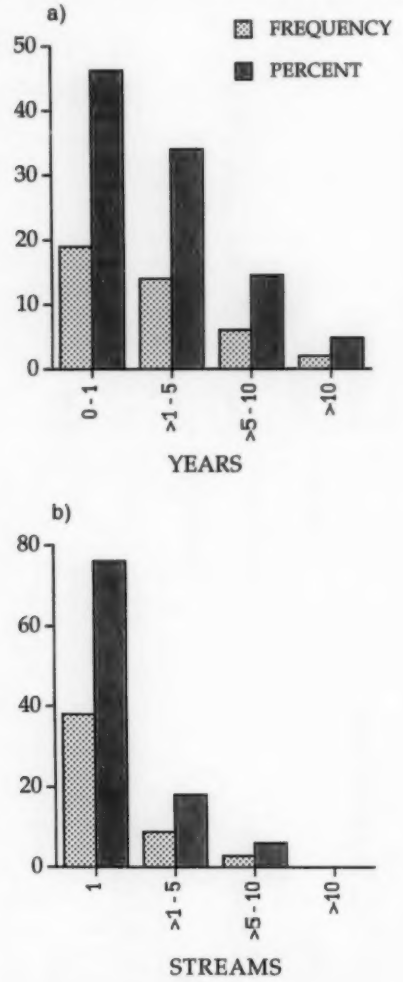
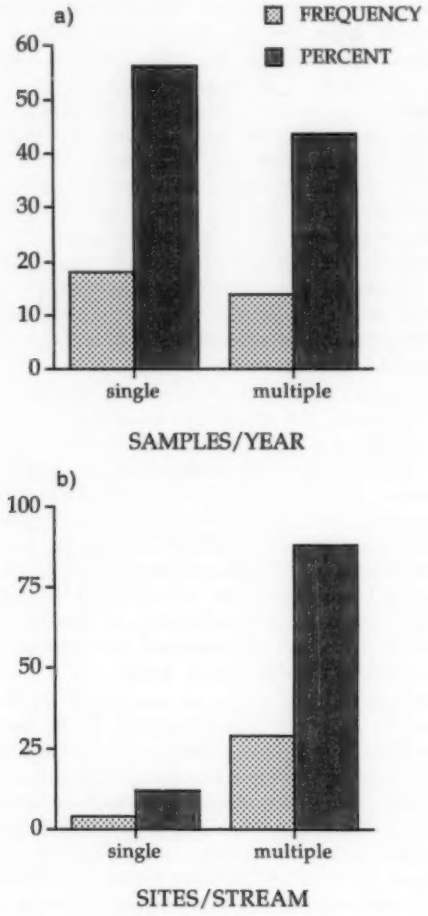


Fig. 4. Frequency and percentage of Atlantic salmon studies conducted at 5 categories of temporal (Fig. 4*a*) and spatial (Fig. 4*b*) resolution. Details of the literature search and classification criteria given in text.



encompassed most of the geographic range of the Atlantic salmon in both North America and Europe (with the exception of the Baltic region) and a wide range of ecological topics (Fig. 2).

The majority of these studies of Atlantic salmon appear to trade increased resolution for reduced spatial and temporal extent. More than 75% of studies were conducted within a single river system, with fewer than 20% lasting for more than 5 years (Fig. 3). However, most studies were relatively fine grained. Greater than 85% of studies included samples taken from multiple locations within a river or single drainage system, and 44% of the studies included samples taken multiple times within the course of a single year (Fig. 4).

Implications of scale bias to Atlantic salmon research

The results of our search indicate that scale-bias is common in Atlantic salmon research. Most studies are limited in their temporal extent and rarely span the life cycle of an individual, or even the change of seasons and its associated change in physical and biological constraints. Choosing the appropriate time scale for each study requires understanding the nature of both the physical and biological features of the system. As pointed out by Frost et al. (1988) the danger lies in selecting a time frame that is either too short or too long. Inferences must be carefully evaluated within a specific temporal framework, which makes comparisons among studies even more challenging. Limitations on temporal extent (study duration) are probably linked in part to limited resources and human-imposed temporal limitations (the

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average duration of a graduate thesis or a funding period). However, the paucity of long-term investigation weakens inferences we can make about processes spanning longer periods and thus our ability to predict long-term trends under changing environmental and human pressures.

There is also a bias in the spatial scale of most Atlantic salmon field investigations. Most studies have concentrated on measuring particular systems (e.g., single river systems, or even single tributaries or reaches within a single tributary) using a multiple locations per river (high-resolution) approach. This emphasis probably reflects the management orientation of a great deal of Atlantic salmon research, which is often directed towards river-specific, applied problems (i.e., is a particular river good or bad for salmon, and why?), and the idiosyncratic nature of research (salmon biologists are placed somewhat haphazardly across the globe, studying the systems nearest to their home base). These intensive studies have been extremely effective at elucidating individual behaviors, genetics, physiology, and many small-scale ecological processes (Schlosser 1991). Yet they are less effective for comparing across systems where different biotic and abiotic factors prevail.

There are great differences in resolution or grain across studies. Methods for censusing populations differ greatly, and whether individuals, reaches, or entire streams are being characterized influences the appropriate spatial scale of the study. As pointed out by Grant et al. (1998), Folt and Schulze (1993), and others, small-scale patchiness, which is generally not characterized in sampling programs, may be fundamental to understanding outcome of important density-dependent interactions. This could be particularly important for understanding interactions among space holding territorial species like Atlantic salmon juveniles, where the precise numbers and sizes and nature of neighbors or food can have a strong impact on individual foraging and overall performance.

Sampling programs that miss small-scale patterns may overlook the fundamental importance of density-dependent processes in salmon population regulation. Ray and Hastings (1996) demonstrate that identifying density-dependent relationships may be especially biased by the spatial sampling design. They argue that the lack of density-dependence observed in many current studies may be an artifact of sampling programs that average over regions of widely varying population density and obscure key relationships. Further, with a study of scale-related dynamics in 79 insect populations, they found that short-time series (low temporal extent) or low test power (fewer samples) were far less important for detecting density-dependence than identifying the appropriate spatial scale.

The effect of differing spatial resolution can be illustrated by comparing predictions from two types of bioenergetic models. These models are used to examine the relationship between resources and performance. They predict fish growth rate potential as a function of both biotic and abiotic aspects of the environment, (e.g., prey density, physical habitat structure) and intrinsic characteristics of individual fish (Hewett and Johnson 1992; Ney 1993). Although they use the same input parameters and the same equations relating environment to growth, the two types of models operate at different spatial scales. "Simple" bioenergetic models are based on average conditions across a lake, river, or (at slightly higher resolution) a reach, while "spatially explicit" bioenergetic models (Brandt et al. 1992) require higher resolution information because they incorporate the actual spatial distribution of fish, their prey, and physical conditions that affect foraging and growth. Spatially explicit and site-averaged models can produce very different predictions. In a revealing example, Brandt and Kirsch (1993) found that for striped bass (*Morone saxatilis*) in Chesapeake Bay, site-averaged growth rate potential was consistently greater than spatially explicit predictions. Their explanation was that prey spatial distribution was highly patchy, and that prey densities in high density patches often exceeded densities that produce the maximum consumption rates of predators. In the spatially explicit version, this important behavioral constraint is modeled. However in the site-averaged model, behavioral restrictions on consumption are not included. In this example, a behavioral mechanism (density dependence in foraging rate) sets a ceiling on consumption, so that resolution of small-scale patchiness becomes necessary to understand the predator–prey dynamics.

Because of limited support for research, increasing sampling grain to the resolution necessary to follow individuals and their neighbors will restrict either the number of sites investigated or the number of times the samples are taken. When populations are especially patchy in space or time, it may be necessary to increase resolution no matter what the "cost." Yet, increased resolution is certainly not always required and in some cases may actually hide other large-scale processes (Frost et al. 1988). Obviously, future studies should be designed with the understanding that the resolution has a strong influence on the inferences that are drawn. A review of new methods for identifying the appropriate scale for specific systems and questions is well beyond the scope of this paper, but methods for matching variance in biological and physical processes are of growing importance to the design of research programs (Horne and Schneider 1994).

Strategies for expanding scale

As discussed above, a powerful technique for identifying the importance of scale is to conduct multiple scale studies, identify scale inconsistencies, and to use a combination of experiments or models to test the underlying mechanisms in order to extrapolate across systems. However, there are also other ways to confront scale issues that are being applied in a number of different research areas. We now address three possible methods to expand scale and test for generality across scales.

Scaling up

High-resolution, low-extent studies are valuable for certain questions. But site and time specificity comes with some costs as it limits the detection of larger scale determinants of potentially important processes. There have been a number of calls recently to "scale up," emphasizing the importance of comparing ecological processes for stream fish across larger spatial or temporal scales (Lewis et al. 1996;

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Cunjak 1996). Concordance in the change in fish abundance among streams in Colorado led Gowan and Fausch (1996) to emphasize the importance of regional (large-scale) processes to fish dynamics. However, comparisons across systems or regions are problematic for a number of reasons, making it clear that scaling up is not simple.

Difficulties of scaling up are particularly apparent when increasing extent is associated with decreasing resolution (coarser grain). For example, salmonid researchers have been debating whether population density in a stream reach is determined by seasonal "self-thinning" processes in relation to some maximum carrying capacity of the environment (Grant and Kramer 1990; Grant 1993; Grant et al. 1998) or, instead, is determined by mortality during a critical period for survival early in ontogeny (Elliott 1989, 1994). Armstrong (1997) used statistical techniques to look at a single dataset (Elliott 1994) with two degrees of temporal resolution — multiple measurements over a year (fine resolution) and single estimates for each year in the dataset (coarse resolution). Armstrong found that the coarse resolution analyses could not isolate an effect of a critical period and suggested the importance of self-thinning processes to density. In contrast, the finer-resolution approach indicated that self-thinning was largely a by-product of early season mortality, which supported the critical period theory for explaining density.

Large-scale studies (e.g., watersheds) are particularly vulnerable to problems in addition to loss of fine scale resolution. Because of logistical considerations, comparable replicates are limited; they may be non-existent in the case of paired watershed studies (Power et al. 1998). At such large scales, it is not at all uncommon for unpredictable events (fires, floods) with high-magnitude impacts to affect either the "control" or the comparison watershed only, largely invalidating the study. These studies also tend to measure highly integrated "output" variables such as stream flow or total production, which are affected by a host of factors, making it difficult to understand the mechanisms by which changes occur (Lewis et al. 1996). Perhaps as a consequence of these limitations, Hicks et al. (1991) found that while watershed scale variables have been associated with salmonid abundance, no two studies have identified the same set of variables as being important, severely limiting the generality of research findings.

Despite these problems, large-scale comparisons are essential for certain questions. For example, recent large-scale studies have revealed important relationships between land use and ecological variables (see references in Schlosser 1991). An approach to conservation of Pacific salmon species has been strongly advocated that requires management of salmon at least at the basin-wide level (Allendorf et al. 1997). For basin-wide management to be effective requires an expansion from single or few sites to sites across the range of habitats and range of conditions within the basin (see Kocik and Ferreri 1998).

Another powerful tool for resolving scale issues is to "scale down" using experiments and models to explore the mechanisms underlying scale inconsistencies and patterns. A number of recent papers have dealt with the appropriate use of experiments and modeling in ecology (Frost et al. 1988; Schlosser 1991; Power et al. 1995, 1998; Osenberg et al. 1998; and others (this issue)) and emphasized their strengths and weaknesses (especially with respect to scale). Laboratory experiments have been widely used to identify a number of behavioral and physiological processes for Atlantic salmon, but field experiments are still relatively uncommon (but see Kennedy and Strange 1986; Whalen and LeBar 1994; Nislow et al. 1998). To effectively test for mechanisms driving inconsistencies or similarities at different scales we should sample at several scales, scaling up where possible and necessary, and combine these measurements with carefully designed experiments or models nested within the sampling program (see reviews by Mather 1998; Fausch 1998; Grant et al. 1998; and others (this issue) for more details on experiments with salmonids).

Synthesis across studies

One of the primary goals of all papers in this issue was to include a review of the literature in order to synthesize among studies and thereby to expand the scale of inference. Most reviews seek to expand the extent and resolution that can be obtained by comparing numerous intensive, and usually small-scale individual studies. There is a growing movement within the field of ecology to do this in a quantitative fashion (Gurevitch et al. 1992; Gurevitch and Hedges 1993; Fernandez-Duque and Valeggia 1993; Arnqvist and Wooster 1995). Different techniques are being proposed, debated, and refined in the literature, including meta-analysis and application of Bayesian statistics (Ellison 1996; Dennis 1996; Osenberg et al. 1998). These techniques appear promising for synthesizing among disparate studies of Atlantic salmon and are likely to result in some fundamental advances in the field when appropriately applied to topics currently under debate.

Meta-analysis has been used by investigators in many different systems to analyze and synthesize a number of independent studies. A key goal of meta-analysis is to extract a quantitative metric (e.g., effect size) from each study and then to apply statistical techniques to the comparison of this metric across studies (Osenberg et al. 1998). Recent meta-analyses include comparisons of the effects of selective logging on density of birds (Fernandez-Duque and Valeggia 1993), of effects of benthic versus drift feeding predators on the density of stream invertebrates (Dahl and Greenberg 1996), and strength of fish–snail interactions across lakes (Osenberg et al. 1998). A number of issues identified in this volume would be suitable for meta-analysis. One difficulty in conducting a meta-analysis arises when the investigations are run on different time or spatial scales, as shown in Osenberg et al. (1998). However, meta-analysis also can be used to test for scale inconsistencies among studies. This information can then be coupled with other approaches (field sampling, experimental manipulation, or modeling).

Following individuals over space and time

Atlantic salmon travel vast distances over time and space, which makes it logistically difficult to follow any individual over its lifetime. Okubo (1980) distinguishes two viewpoints or approaches for investigating moving populations. The first is the LaGrangian approach, which follows a population

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or an individual through space. The second is the Eulerian approach, which is to watch individuals or populations flow past a fixed point or through a fixed area.

Movements by Atlantic salmon impose logistic constraints on following individuals, even within a single habitat during a single life history stage (Armstrong et al. 1994). These constraints severely restrict the use of the LaGrangian technique. In studies of Atlantic salmon, it has been more common to take a Eulerian approach and to observe a number of individuals in an "instant" in time (e.g., by censusing all individuals in a reach or counting smolt moving past a counting station, etc.). Even when reaches are sampled repeatedly, individuals are rarely distinguished.

The Eulerian approach is appropriate for many questions, and carries with it the need to make many strategic decisions about extent and resolution in the sampling design, because the temporal and spatial scale of the study is essentially imposed by the researcher (as discussed previously). Adopting a LaGrangian perspective would enhance our ability to approach a number of questions in population and community ecology that cannot be addressed by Eulerian methods, in large part because LaGrangian approaches allow the organism to define the relevant scale. For example, long-term studies by Connell et al. (1997) on coral reef communities employ an essentially LaGrangian approach. He has followed individuals for more than 25 years, making it possible to examine the cumulative effects of species interactions and physical processes on growth and survival over the lifetime of an individual. This approach has been very successful in understanding the ecology of these sessile communities.

In situations where it is difficult or impossible to mark and follow individuals, modeling dispersal processes can allow researchers to simulate a LaGrangian approach for investigating habitat and population dynamics. For example, Bozek and Rahel (1991) found a scale inconsistency in habitat resource tracking in juvenile cutthroat trout. Within stream reaches, individuals preferred slow, deep microhabitats, but shallow reaches with abundant spawning gravel had the highest trout abundances. The low abundance or total absence of juvenile trout in stream reaches that seemed to contain suitable microhabitats appeared to result from spawning gravel limitation, explaining the scale inconsistency. Reaction-diffusion, or diffusion/dispersal models (Turchin and Thoeny 1993), which model distance-dependent dispersal success from a point source (such as a salmonid redd or a rearing tributary mouth) may therefore allow integration across spatial scales and improve our ability to predict salmonid abundance and survival in the context of these critical demographic events.

Even when mobile individuals can be marked and followed, the intensity of effort per individual restricts sample sizes (limits resolution) and generally forces inferences to be drawn from a few individuals in a few circumstances. Yet new techniques are being applied to the study of Atlantic salmon that will allow a more LaGrangian approach to be applied to larger samples of fish. For example, microsatellite genetic markers have been already developed to mark large numbers of individuals (Letcher and King 1997). Identity (from parentage) of an individual can be determined from a single fin clip, so individuals can be sampled repeatedly during their lives. This technique will eventually be applied to many questions (e.g., How far do individuals move during the stream phase? Which individuals (based on parentage or stocking location) are the successfully returning adults?) Fingerprinting salmon via stable isotopes of strontium and nitrogen has also been shown to be effective for following movements of groups of individuals over time (Kennedy et al. 1997; Harrington et al. 1998). Using organism structures that record the history of individuals, for example, growth rings on fish otoliths (Wright et al. 1990) is a third technique that can be used to follow an individual over time. Perhaps the most powerful developments will arise from combinations of these new techniques, which may allow large numbers of salmon to be followed from birth to death and to address questions not possible with other methods.

Summary and conclusions

The "great scale problem," as stated by Fahrig (1992) is, "what is the appropriate scale for study of a particular problem?" This is not a simple question for Atlantic salmon, because as we have seen, the mechanisms linking salmon and their environment vary over long and short times and over large and small spatial scales. We suggest that identifying scale inconsistencies via multiple scale observations and measurements is the first step for identifying the scales over which processes affecting distribution and abundance operate. Strategic use of experiments and models and expanded quantitative analysis of different studies using meta-analysis are likely to greatly enhance our understanding. Finally, application and development of new technologies that allow new approaches to old questions are certain to reveal novel insights that will contribute to the effective conservation and management of the Atlantic salmon worldwide.

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Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*

Jeffrey A. Hutchings and Megan E.B. Jones

Abstract: Based upon published and unpublished data compiled for 275 populations, we describe large-scale spatial and temporal patterns in Atlantic salmon, *Salmo salar*, life history and model these data to evaluate how changes to life history influence optimal growth rate thresholds for sea age at maturity. Population means (ranges in parentheses) describe the following for salmon throughout its range: smolt length = 14.8 cm (10.5–21.5 cm); smolt age = 2.91 years (1.04–5.85 years); egg-to-smolt survival = 1.5% (0.2–3.2%); grilse length = 56.8 cm (48.5–70.0 cm); sea age at maturity = 1.60 years (1.00–2.64 years); smolt-to-grilse survival = 7.4% (1.3–17.5%). Growth rate thresholds specify the length increase between the smolt and grilse stages above which reproduction after one winter at sea is favoured over later maturity. Our simulations indicated that increased growth generally favours earlier, but never delayed, maturity. Optimal growth rate thresholds for sea age at maturity are highly sensitive to survival but only moderately sensitive to fecundity, smolt size, and smolt age. Depending on an individual's growth rate at sea, early maturity is favoured by decreased smolt age or by increased smolt length, fecundity, or survival (freshwater or marine). We suggest that future Atlantic salmon life history research focus upon reaction norms and growth rate thresholds for age at maturity, demographic and genetic consequences of male parr maturation, and the origin and maintenance of coexisting anadromous and nonanadromous life history polymorphisms.

Résumé : À partir de données publiées et non publiées relatives à 275 populations, nous décrivons des profils spatiaux et temporels à grande échelle du cycle vital du saumon de l'Atlantique, *Salmo salar*, et modélisons ces données pour évaluer comment les changements dans le cycle vital influent sur les seuils de taux de croissance optimaux relatifs à la durée du séjour en mer avant la maturité. Les moyennes (fourchettes entre parenthèses) de divers paramètres des populations du saumon dans l'ensemble de son aire de répartition sont les suivantes : longueur des smolts = 14,8 cm (10,5-21,5 cm); âge des smolts = 2,91 ans (1,04–5,85 ans); taux de survie de l'oeuf au stade de smolt = 1,5 % (0,2–3,2 %); longueur des grilses = 56,8 m (48,5–70,0 cm); durée du séjour en mer avant la maturité = 1,60 an (1,00–2,64 an); taux de survie du smolt au grilse = 7,4 % (1,3–17,5 %). Les seuils de taux de croissance indiquent l'accroissement de longueur du stade de smolt au stade de grils au-delà duquel la reproduction après un hiver en mer est favorisée par rapport à une maturité plus tardive. Nos simluations ont indiqué qu'une croissance accrue donne généralement lieu à une maturité hâtive, et jamais à une maturité retardée. Les seuils de croissance optimaux relatifs à la durée du séjour en mer avant la maturité sont hautement sensibles à la survie, mais seulement modérément sensibles à la fécondité, à la taille des smolts et à l'âge des smolts. Selon le taux de croissance individuel en mer, la maturité sera atteinte plus rapidement plus l'âge des smolts est bas et plus la longueur, la fécondité et le taux de survie (eau douce ou eau salée) de ces derniers sont élevés. Nous proposons de concentrer les recherches futures concernant le cycle vital du saumon atlantique sur les normes de réaction et les seuils de taux de croissance relatifs à la durée du séjour en mer avant la maturité, sur la démographie et les conséquences génétiques de la maturation des tacons mâles, et sur l'origine et le maintien des polymorphismes coexistants dans les cycles vitaux anadromes et non anadromes.

[Traduit par la Rédaction]

Introduction

Life history variation in Atlantic salmon, *Salmo salar*, is matched by few vertebrates. Age at maturity ranges one order of magnitude from 1 year for male parr in France (Baglinière and Maisse 1985) to 10 years for some anadromous salmon in northern Québec (Power 1969; Robitaille et al. 1986). Size at maturity varies 14-fold from less than 7 cm for males in Newfoundland rivers (Hutchings 1986; Gibson et al. 1996) to more than 100 cm for females in Norway's River Vosso (Huitfeldt-Kaas 1946). Fecundity can vary 500-fold from fewer than 40 eggs per female in wholly freshwater populations (Gibson et al. 1996) to 18 000 eggs per female in anadromous populations (e.g., Margaree River, Nova Scotia; Canadian Department of Fisheries and Oceans (DFO) unpublished data). Offspring size, measured as egg volume, varies more than three-fold from 48 mm^3 for landlocked salmon, or ouananiche, (4.5 mm egg diameter; Gibson et al. 1996) to 171 mm^3 in anadromous individuals (6.9 mm diameter for salmon in Restigouche River, New Brunswick/Québec; DFO unpublished data).

Since the early experimental (e.g., Shaw 1836) and descriptive work on Atlantic salmon life histories in Europe (e.g., Brown 1862; Mieschер-Rusch 1883; Calderwood 1906; Dahl 1910) and in North America (Atkins 1884;

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J.A. Hutchings and M.E.B. Jones. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

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Chambers 1896; Huntsman 1931), considerable research has been directed to identifying the causal basis for population differences in the ages at which salmon migrate to and return from the sea (e.g., Schaffer and Elson 1975; Power 1981; Myers and Hutchings 1987; Metcalfe and Thorpe 1990; see also the review by Gardner (1976) and the papers contained in Meerburg (1986)), and for population differences in the incidence of early maturity among males (e.g., Jones 1959; Thorpe 1975; Thorpe et al. 1983; Myers 1984; Myers et al. 1986; Hutchings and Myers 1988, 1994; see review by Fleming 1996). Within this research milieu, our objectives were to describe spatial and temporal life history variation throughout the geographical range of Atlantic salmon and, using the life history trait associations that emerged, to predict optimal responses in sea age at maturity effected by changes to growth rate and survival.

Naturally reproducing Atlantic salmon exist throughout the North Atlantic coasts from Maine to northern Labrador in North America, throughout Iceland, Ireland, and Great Britain, and in mainland Europe from northern Spain to the Kara River, Russia (Berg 1948; Nielson 1961; Scott and Crossman 1973). Anadromous individuals typically spend 20–50% of their life at sea; nonanadromous populations spend their entire life in fresh water. Females bury fertilized eggs in the substrate of freshwater rivers and streams in autumn. After hatching, the young obtain nourishment from a yolk sac before emerging from the substrate in spring. After periods of usually 1 to 5 years in fresh water as parr, anadromous individuals emigrate as smolts and generally spend 1 or 2 (rarely 3 or 4) years at sea before returning to fresh water to spawn. In populations for which migration to sea is not prevented by physical barriers, females are usually anadromous, although there are numerous exceptions in Newfoundland (Hutchings 1986) and some elsewhere (Baglinière and Masse 1985; also see Fleming 1996). In contrast, males often reproduce after 1 to 4 years in fresh water, after which they may or may not migrate to sea. Estimates of postreproductive, overwinter survival for mature male parr range from less than 15% (calculated from Hutchings 1985, 1986) to 40% (Myers 1984; Hutchings and Myers 1994); those for anadromous males and females are often less than 15% (Bley and Moring 1988).

There are several means by which one can practically assess the adaptive significance of life history variation in fish, each with its limitations and advantages. These include field (e.g., Reznick et al. 1990; Fleming and Gross 1993) or laboratory manipulation experiments (e.g., Metcalfe et al. 1989; Hutchings 1991), within- (e.g., Riddell and Leggett 1981; Sandlund et al. 1992) and among-population comparisons in the field (e.g., Leggett and Carscadden 1978; Hutchings 1993; Fox 1994), and analyses of data from the literature on life history differences within and among species (e.g., Beverton and Holt 1959; Schaffer and Elson 1975; Roff 1984; Hutchings and Morris 1985). We adopt the last of these to describe and analyse Atlantic salmon life history variation throughout the species' geographical range.

An extensive among-population study allows one to examine life history differences throughout the entire range of variation expressed by a species, thus encompassing the boundaries or potential limits of phenotypic variation. As a consequence, among-population correlations between life history traits can delineate phenotypic patterns to which any general life history model of Atlantic salmon should ascribe (Marschall et al. 1998). Limitations to analyzing data from the literature include practical issues such as (1) an inability to quantify measurement errors, (2) unknown sample sizes, and (3) varying numbers of years and time periods over which population means are estimated. There is also the theoretical caveat that associations between life history traits at the population level need not reflect natural selection. This is why we supplemented our analyses with empirically based simulations to predict optimal life history responses within populations.

Data analysis

Published and unpublished data were compiled for 13 life history-related variables for 275 Atlantic salmon populations (Table 1; Appendices 1–2) and grouped by region: U.S.A., Québec, Newfoundland, Canadian Maritimes, Iceland, Ireland, Great Britain, mainland Europe, Norway, Sweden, Russia. Naturally, there are a number of means by which populations could be classified. One could argue, for example, that latitudinal groupings might be appropriate. However, given the extraordinary life history variation in salmonids that can exist within narrow ranges of latitude, e.g., incidence of male parr maturity in Atlantic salmon (Myers et al. 1986), survival and egg size in brook trout, *Salvelinus fontinalis* (Hutchings 1991, 1993), and age and size at maturity in Arctic char, *S. alpinus*, (Skúlason et al. 1998), even traditional latitudinal classifications can be problematic. The geographical categories in which we have grouped salmon populations approximate those used by national (e.g., Canada's DFO) and international (e.g., ICES) management agencies.

Rather than depicting the current status of specific populations, the data presented in Appendix 1 are intended to reflect the range of natural variation in Atlantic salmon life history. For many populations, data have been obtained from comparatively recent statistics (e.g., Newfoundland populations, 1950s to 1990s), for others they have not (e.g., England, 1920s to 1950s). With few exceptions (e.g., the American populations), data were collated for populations that are maintained by naturally reproducing salmon. Our data compilation should not be considered exhaustive; there are assuredly data in the secondary literature that we have overlooked. It might be advantageous to use the present initiative as a basis for constructing a web site devoted to Atlantic salmon population data worldwide.

Box-and-whisker plots were used to illustrate geographical differences in life history. These plots are particularly useful for such a comparison because they allow for simple visual inspection of medians (indicated by a bar in each box; Figs. 1–6), data composition (the lower and upper ends of each box represent the 25% and 75% quartiles, respectively), skewness (the position of the median relative to the ends of each box), and data range (the "whiskers" represent lines extending from the top and bottom of each box to adjacent data no more than 1.5 times the inter-quartile range; values beyond this range are indicated by solid circles).

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Table 1. Geographical areas and number of populations included in the among-population life history analyses.

Region	Number of populations	Subregion	Number of populations by subregion
Iceland	78		
Newfoundland (Canada)	51	Newfoundland	47
		Labrador	4
Norway	37		
Québec (Canada)	36		
Maritimes (Canada)	19	Nova Scotia	10
		New Brunswick	9
Great Britain	18	Scotland	13
		England and Wales	5
Europe	15	France	11
		Spain	4
United States	8		
Ireland	6		
Sweden	5		
Russia	2		
Finland	1		
Total	275		

One-way analysis of variance was used to assess the significance of regional differences in life history trait means, calculated as the average of population means within a given region (Table 2). The regions included in each analysis depended upon data availability. Statistical significance was based upon 1000 randomizations of the data (Manly 1991).

Smolt-to-grilse survival estimates were modified to reflect population differences in sea age at maturity. Unless a population is composed entirely of grilse (i.e., 1SW salmon), survival estimates based upon the numbers of returning grilse relative to the number of smolts that emigrated the previous year will underestimate smolt-to-grilse survival. This is because some proportion of smolts are "pre-determined" to return as multi-sea-winter fish. To account for this bias, we divided reported smolt-to-grilse survival estimates by the percentage of grilse in the population. It should be noted, however, that our estimates of percent grilse (i.e., (n grilse) / (n grilse + n multi-sea-winter salmon)) will be overestimated with the degree of overestimation declining with the true percentage of grilse in a population. The reason for this overestimation is the absence of data on the number of multi-sea-winter salmon that died prior to returning to their natal river. In addition to these caveats, survival estimates for salmon at sea include natural and fishing mortality. Thus, the smolt-to-grilse survival data used here probably underestimate true survival at sea.

To examine how various life history traits and growth rate at sea combine to influence optimal sea age at maturity, we estimated fitness, r, from the discrete-time version of the Euler-Lotka equation,

$$(1) \qquad 1 = \sum_{x=\alpha}^{x=\omega} l_x m_x e^{-rx}$$

where, for ages x between maturity α and death ω, l_x represents the survival probability from birth to the beginning of the spawning season at age x, and m_x represents the number of zygotes produced by an individual spawning at age x. Given the paucity of fecundity and survival data for the same population, we examined how changes to single life history traits influence optimal sea age at maturity by holding the remaining traits constant at values equal to the grand means across all populations. These grand means, and their respective population minima and maxima, are given in Table 3.

Age-specific fecundities, m_x, were calculated using the fecundity–length relationship intermediate among those reported in Fleming's (1996) review, i.e., the relationship between fecundity (F) and length (L, cm) reported for Scotland's River Dee: $F = 0.4667\ (L^{2.2018})$. The length of fish remaining two winters at sea was assumed to be 20 cm longer than the length of grilse (20 cm being the average difference in length between grilse and 2SW fish among all populations in the present data set). To generate differences in fecundity in our simulations, we held the exponent of the fecundity–length regression model constant at 2.2 and varied the intercept (there was no appreciable difference in the results when holding the intercept constant and varying the exponent).

In our model, survival of 2SW salmon from the smolt stage was set at 55% the survival from the smolt to the grilse stages (55% being the average survival difference reported for a tributary of the Miramichi River; Cunjak and Therrien 1998). Optimal associations between growth rate at sea (approximated by the difference between smolt and grilse lengths) and sea age at maturity were calculated for the minimum (0.013), average (0.074), and maximum (0.175) smolt-to-grilse survival probabilities reported in Appendix 1. The sensitivity of our simulations to our parameter estimates is evident from the model's graphical results.

To normalize the data and to remove any effect of the mean on the variance, we transformed original data before

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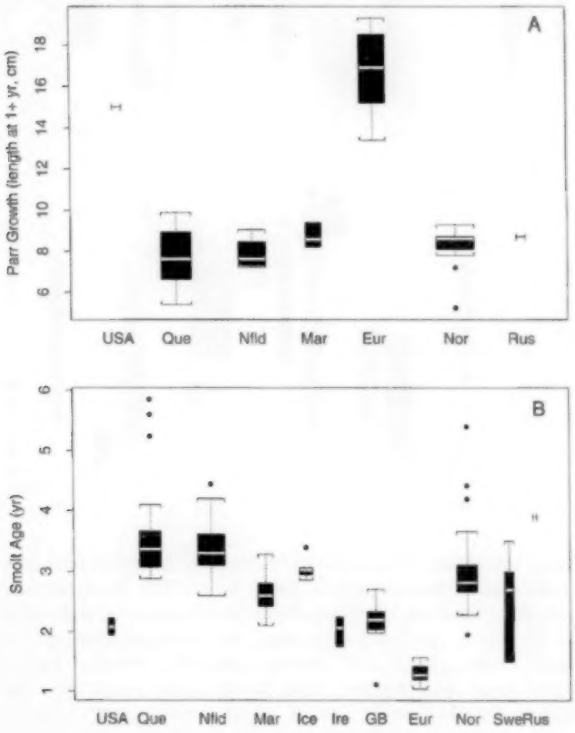
Fig. 1. Box-and-whisker plots of parr growth rate (A) and smolt age (B) for Atlantic salmon throughout its geographical range. Explanation of plots: medians are represented by the white bar in each box; the lower and upper ends of each box represent the 25% and 75% quartiles, respectively; skewness is reflected by the position of the median relative to the ends of each box; the "whiskers" represent lines extending from the top and bottom of each box to adjacent data no more than 1.5 times the interquartile range with values beyond this range indicated by solid circles; the width of each box is proportional to the square root of the number of populations represented in each sample. Sample sizes for each region are given in Table 2.



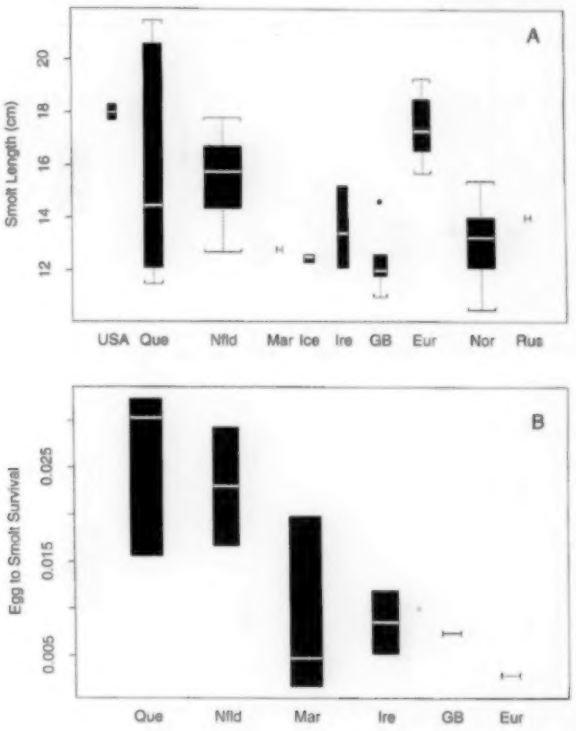
estimating temporal variation in life history traits (Sokal and Rohlf 1981; Appendix 2). The variances of proportional data (i.e., survival, percentage grilse, grilse sex ratio) were calculated from original proportions, p, transformed as $\arcsin(p^{1/2})$; variances of non-proportional data were calculated from $\log_e$-transformations of the original data.

Results

Regional differences in Atlantic salmon life history

Regional differences in age-specific parr length were accentuated by the rapid growth experienced by mainland European populations (Fig. 1A) in which parr aged 1+ year averaged 17.2 cm in length compared to the non-significant differences among Canadian and Norwegian populations for which regional differences in 1+ year parr length ranged, on average, between 7.8 and 8.8 cm (Table 2). The minimum and maximum parr lengths at age 1+ year for single popula-

Fig. 2. Box-and-whisker plots of smolt length (A) and survival from the egg to smolt stages (B) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.



tions were documented for Norway's Beiarelva (5.2 cm) and France's Adour (19.3 cm), respectively (Appendix 1).

Smolt age differed significantly among regions (Fig. 1B), ranging from a mean of 1.29 years for European populations to 3.36 and 3.60 years for Newfoundland and Québec populations, respectively (Table 2). Population mean smolt age ranged from 1.04 years (Nivelle, France) to 5.85 years (George, Québec) (Appendix 1). Among the 94 populations for which data were available, smolt age was uncorrelated with smolt length ($r = -0.13$, $p = 0.24$), the latter varying among regions from an average 12.4 and 12.5 cm for British and Icelandic populations, respectively, to 17.6 and 18.0 cm for European and American populations, respectively (Table 2, Fig. 2A). Among populations, smolt length ranged from 10.5 cm (Nummedals, Norway) to 21.5 cm (George, Québec) (Appendix 1).

Survival during the freshwater stage is usually estimated as the proportion of eggs in a cohort that survive to migrate to sea. The uncertainty associated with this estimate may be considerably greater than that associated with other life history variables. This is because of the numerous parameters, each with an associated measurement error, and many assumed invariant among years, used to estimate egg deposition (e.g., number of females, number of eggs per female, sex ratio of anadromous adults, female weight). Notwithstanding these caveats, there was no significant difference in

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Fig. 3. Box-and-whisker plots of length of 1SW salmon (A) and growth rate at sea (the differences between lengths of smolts and 1SW salmon) (B) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.

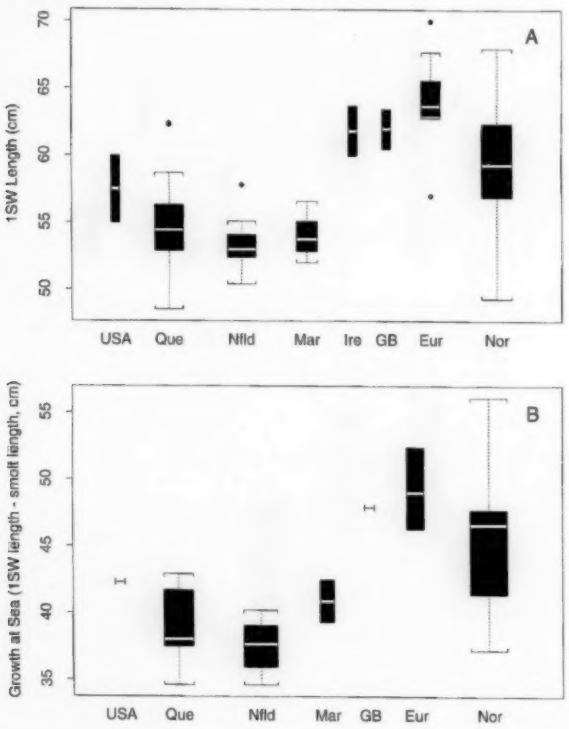
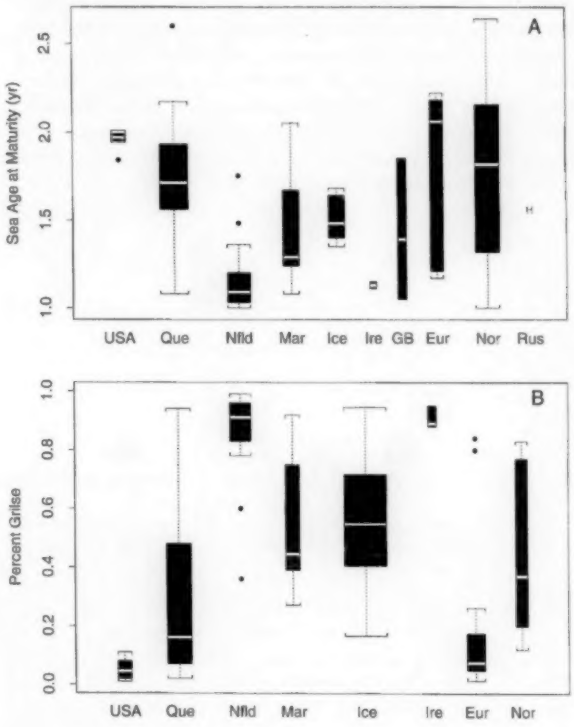


Fig. 4. Box-and-whisker plots of sea age at maturity (A) and percentage of grilse (B) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.



egg-to-smolt survival among regions (Table 2, Fig. 2B). Although sample sizes were small and the range in estimates within regions large, data indicate that mean freshwater survival is highest in Newfoundland and Québec (0.023 and 0.026, respectively) and lowest among Northeast Atlantic populations, ranging from 0.003 to 0.009. Accounting for regional differences in mean smolt age, annual survival probabilities in fresh water ranged from 0.01 in Europe to 0.33 in Newfoundland and Québec (other estimates include 0.15 (Maritimes), 0.10 (Great Britain), and 0.09 (Ireland)).

Growth rate at sea can be approximated as the difference between the lengths of smolts and grilse. The latter differed by 20% among regions (Fig. 3A, Table 2) being lowest in the western North Atlantic (regional averages of 53.2, 54.3, and 54.7 cm for Newfoundland, Maritime, and Québec populations, respectively) and highest in the eastern North Atlantic (e.g., 62.0 and 64.1 cm for British and European populations, respectively). On average, the smallest grilse were those in Québec's Jupiter (48.5 cm) with the largest being those in Spain's Narcea (70.0 cm) (Appendix 1). Average length gained at sea between the smolt and grilse stages differed significantly among Newfoundland (37.4 cm), Québec (38.8 cm), Maritimes (40.9 cm), Norway (45.9 cm), and Europe (49.2 cm) (Fig. 3B).

Mean sea age at maturity differed significantly among regions (Fig. 4A). Comparing the extremes (Table 2), American (1.96 years), Norwegian (1.83 years), and mainland European (1.81 years) salmon spend 60 to 70% more time at sea than those in Newfoundland (1.15 years) and Ireland (1.13 years). Among populations, the youngest average sea ages were those for Newfoundland's Wings Brook (1.00 year) and Western Arm Brook (1.01 years) and the oldest for Norway's Vosso (2.58 years) and Årøelva (2.64 years) (Appendix 1). Among regions, the average incidence of grilse ranged from 5% for American populations to 86 and 91% for Newfoundland and Ireland populations, respectively (Table 2, Fig. 4B). The female sex ratio of returning grilse, varying from 5% (Québec) to 67% (Newfoundland), also differed significantly among regions (Fig. 5A, Table 2). Average smolt-to-grilse survival, highest in the Maritimes (0.130) and lowest in Iceland (0.010), did not differ significantly among regions, although sample sizes were low and the range in population estimates within regions high (Table 2, Fig. 5B).

Salmon age at maturity (smolt age plus sea age plus 1 year, to ensure that total age represented absolute time between an individual's fertilization and spawning) differed significantly among regions ($p < 0.001$) (Table 2, Fig. 6). The oldest average ages at maturity were found in Québec (6.27 years; species' population maximum of 8.80 years in George), Norway (5.71 years), and Newfoundland (5.58 years) with the youngest observed in Great Britain (4.58 years), mainland Europe (4.08 years; species' popula-

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Fig. 5. Box-and-whisker plots of the percentage of grilse that are females (A) and adjusted survival between the smolt and grilse stages (B) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.

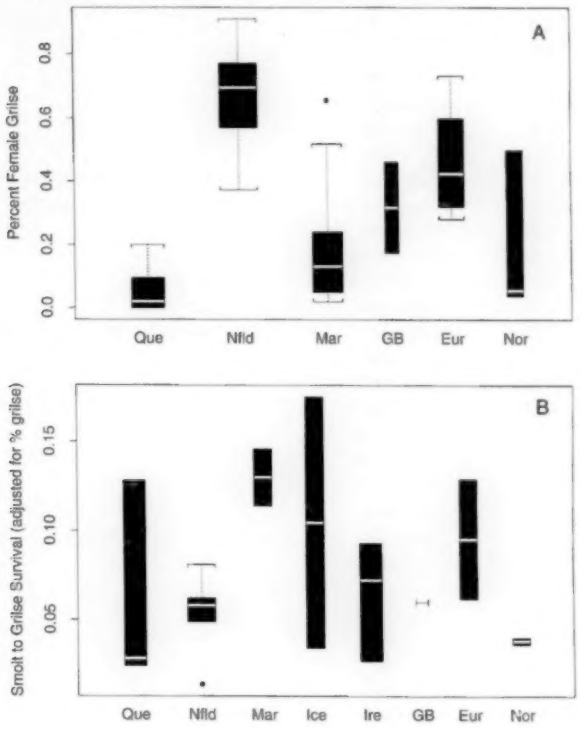
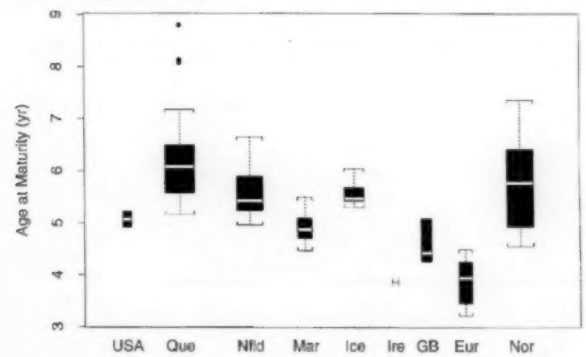


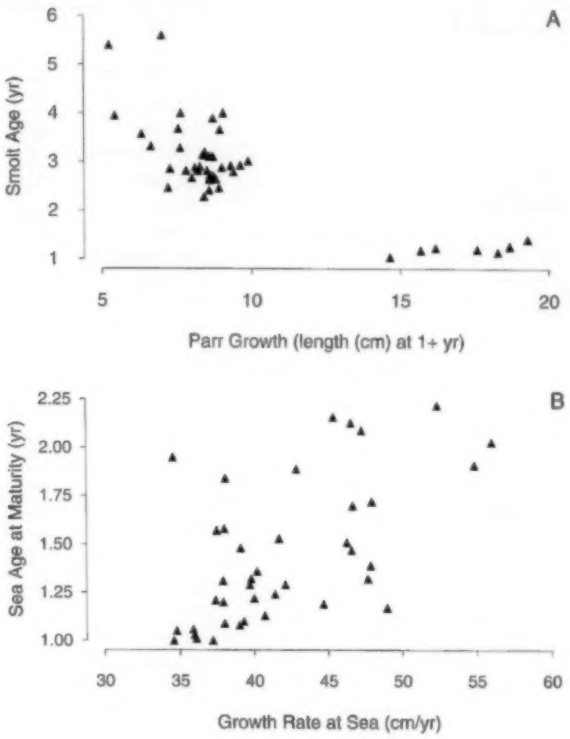
Fig. 6. Box-and-whisker plot of age at maturity (smolt age plus sea age plus 1, see text for further details) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.



tion minimum of 3.21 years in Nivelle), and Ireland (3.86 years).

The freshwater residence period of anadromous salmon declined with increasing parr growth at the population level ($r = -0.79$, $p < 0.001$; Fig. 7A). In addition to being the primary determinant of smolt age, previous work suggests that parr growth rate is also positively associated with the incidence of male parr maturity (Myers et al. 1986; Thorpe 1986) which differs significantly among Canadian populations, ranging from an average of 22% for Québec populations to 57% in Newfoundland (Appendix 1, Table 2).

Fig. 7. Scatterplots between smolt age and parr growth (length at age 1+ year) (A) and between sea age at maturity and growth rate at sea (B) for Atlantic salmon populations throughout the species' range.



Time spent at sea, a major component of age at maturity for anadromous salmon, was positively associated with growth rate at sea among populations ($r = 0.47$, $p = 0.002$; Fig 7B). Sea age at maturity was not correlated with post-smolt survival at the population level ($r = -0.17$, $p = 0.254$).

Predicted optimal associations among growth rate, survival, and sea age at maturity

Empirically based model simulations provide one means of identifying optimal associations among growth rate, survival, and sea age at maturity. A primary feature of the results of these analyses (Figs. 8–10) is the characterization of growth rate thresholds for sea age at maturity, i.e., the 1-year increase in length between the smolt and grilse stages that favours reproduction after one rather than two winters at sea.

Age and length at smoltification appear to have comparatively small influence on optimal growth rate thresholds for sea age at maturity (Fig. 8A–F). The primary effects of increases in smolt age and smolt length are increases and declines in growth rate thresholds, respectively, over comparatively small ranges of 5 to 10 cm·year^{-1}. Increased 1SW survival (i.e., smolt-to-grilse survival) reduces growth

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Table 2. Regional means of Atlantic salmon life history traits and associated ANOVA results. Means represent averages among populations (n) within regions; standard deviations are those for the regional means; population averages represent means across years of available data.

Trait	Region	Mean	SD	n	p
Parr length at 1+ year (cm)	Europe	16.7	2.1	8	<0.001
	U.S.A.	15.0	—	1	
	Maritimes	8.8	0.6	3	
	Russia	8.7	—	1	
	Norway	8.3	0.9	17	
	Newfoundland	7.9	0.7	9	
	Québec	7.8	1.4	11	
Smolt age (years)	Russia	3.90	—	1	<0.001
	Québec	3.60	0.79	27	
	Newfoundland	3.36	0.45	45	
	Iceland	3.03	0.13	11	
	Norway	3.01	0.74	25	
	Finland	2.70	—	1	
	Maritimes	2.59	0.33	13	
	Sweden	2.44	0.90	5	
	Great Britain	2.18	0.35	17	
	U.S.A.	2.08	0.20	2	
	Ireland	2.02	0.25	3	
	Europe	1.29	0.15	13	
Smolt length (cm)	U.S.A.	18.0	0.4	2	<0.001
	Europe	17.6	1.4	6	
	Newfoundland	15.5	1.4	38	
	Québec	15.5	3.9	10	
	Russia	14.0	—	1	
	Ireland	13.6	1.6	3	
	Maritimes	13.4	0.8	2	
	Norway	13.1	1.2	22	
	Iceland	12.5	0.2	3	
	Great Britain	12.4	1.4	5	
Egg-to-smolt survival	Québec	0.026	0.010	3	0.25
	Newfoundland	0.023	0.009	2	
	Maritimes	0.009	0.010	3	
	Ireland	0.009	0.005	2	
	Great Britain	0.007	—	1	
	Europe	0.003	—	1	
Grilse length (cm)	Europe	64.1	3.4	10	<0.001
	Great Britain	62.0	2.1	2	
	Ireland	61.8	2.6	2	
	Norway	59.5	4.3	25	
	U.S.A.	57.5	3.5	2	
	Québec	54.7	3.5	22	
	Maritimes	54.3	1.5	12	
	Newfoundland	53.2	1.6	22	
Sea age (years)	U.S.A.	1.96	0.50	8	<0.001
	Norway	1.83	0.51	24	
	Europe	1.81	0.44	8	
	Québec	1.72	0.33	33	
	Russia	1.56	—	1	
	Iceland	1.50	0.12	11	
	Maritimes	1.43	0.33	11	
	Great Britain	1.43	0.40	3	
	Newfoundland	1.15	0.17	23	
	Ireland	1.13	0.03	2	
% Grilse	Ireland	0.91	0.04	3	<0.001
	Newfoundland	0.86	0.15	20	

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Table 2. (*Concluded*).

Trait	Region	Mean	SD	*n*	*p*
	Great Britain	0.80	—	1	
	Iceland	0.58	0.19	78	
	Russia	0.53	—	1	
	Maritimes	0.52	0.24	12	
	Norway	0.44	0.27	7	
	Québec	0.32	0.28	27	
	Europe	0.20	0.27	14	
	USA	0.05	0.04	8	
% Female grilse	Newfoundland	0.67	0.15	16	<0.001
	Europe	0.47	0.16	7	
	Great Britain	0.32	0.20	2	
	Maritimes	0.21	0.21	10	
	Norway	0.20	0.26	3	
	Québec	0.05	0.07	12	
Smolt-to-grilse survival	Maritimes	0.130	0.02	2	0.354
	Europe	0.095	0.047	2	
	Newfoundland	0.073	0.027	5	
	Québec	0.060	0.059	3	
	Ireland	0.060	0.047	2	
	Great Britain	0.060	—	1	
	Norway	0.038	0.003	2	
	Iceland	0.010	0.010	2	
Age at maturity (yr)	Québec	6.27	0.95	24	<0.001
	Norway	5.71	0.81	20	
	Newfoundland	5.58	0.46	19	
	Iceland	5.54	0.21	11	
	USA	5.07	0.21	2	
	Maritimes	4.91	0.36	6	
	Great Britain	4.58	0.44	3	
	Europe	4.08	0.51	8	
	Ireland	3.86	—	1	
% Mature male 1+ parr	Newfoundland	0.57	0.31	9	0.024
	Maritimes	0.53	0.27	3	
	Québec	0.22	0.22	10	
	Russia	0.10	—	1	

Table 3. Age (yr)-specific schedules of survival and fecundity used to estimate optimal sea age at maturity in Atlantic salmon.

		Population	
Trait	Average	Minimum	Maximum
Smolt length (cm)	14.8	10.5	21.5
Smolt age (yr)	3.5	1.0	5.8
Egg-to-smolt survival	1.5%	0.2%	3.2%
Smolt-to-grilse survival	7.4%	1.3%	17.4%

rate thresholds for maturation as grilse, irrespective of smolt age or length.

In contrast to smolt age and size, survival in fresh water (i.e., egg-to-smolt survival) has a strong influence on optimal growth rate thresholds for maturity (Figs. 9A–C). A decline in freshwater survival is associated with an increase in the growth rate required for maturity after 1 sea winter to be favoured over maturity after 2 winters at sea. If survival in both fresh water and the sea is low (Fig. 9A), females are favoured to mature as 2SW fish, independent of growth rate. Similarly, if survival in both fresh water and the sea is high, maturation as grilse is favoured (Fig. 9C).

The effect of a decline in smolt-to-grilse survival on growth rate thresholds is similar to that produced by a decline in freshwater survival — increased survival at sea reduces the growth rate at which early maturity is favoured over delayed maturity (Figs. 9D–F). The main effect of an increase in the sea survival of grilse relative to that of 2SW salmon is also a decline in the growth rate threshold for maturity.

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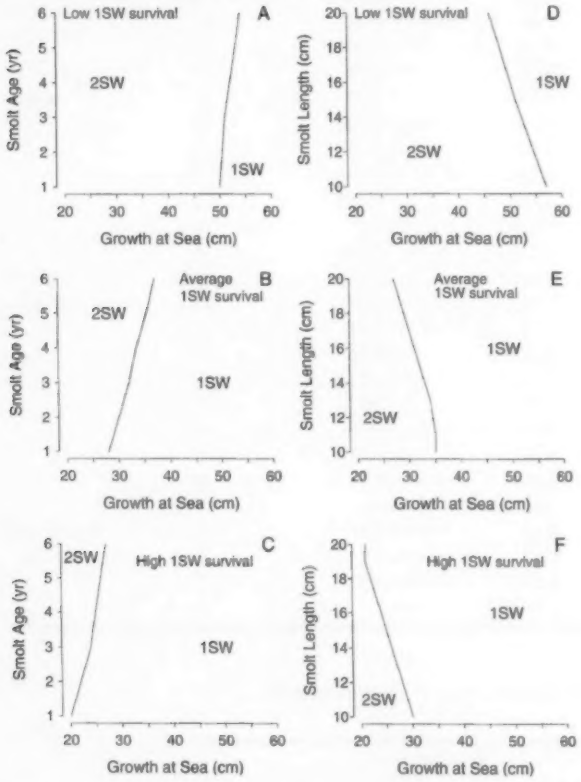
Fig. 8. Effect of smolt age (A–C) and smolt length (D–F) on growth rate thresholds for sea age at maturity in female Atlantic salmon at low (0.0135), average (0.0740), and high (0.1740) rates of smolt-to-grilse survival. Growth rate thresholds, identified by continuous lines in each bivariate plot, identify the growth rate at sea, approximated here as the difference in length between smolts and grilse, that must be exceeded for maturity after one winter at sea (1SW) to be favoured (i.e., have a higher fitness, *r*) over the strategy of maturing after two winters at sea (2SW). Thus, combinations of smolt age or smolt length and growth at sea that lie to the right of each line are those that favour maturity after one winter at sea; those to the left of each line favour maturity after two winters at sea.

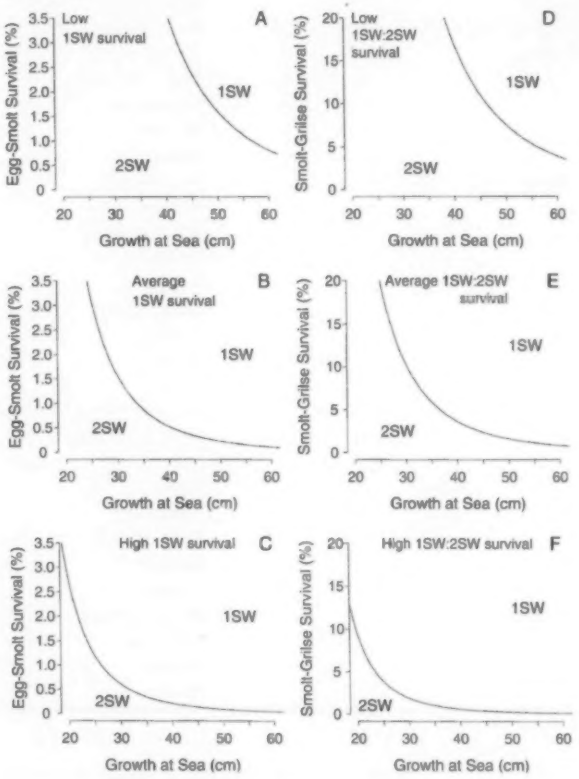


Within the two-fold range of 1500 to 3000 eggs per 50-cm female, as calculated for Atlantic salmon from the regressions given by Fleming (1996), fecundity appears to have comparably little effect on growth rate thresholds for sea age at maturity, being of import within growth rates of 10 cm yr^{-1} or less (Fig. 10). Again, an increase in 1SW survival is predicted to favour earlier maturity, the reduction in growth rate threshold being largely independent of fecundity.

Temporal variation in life history

To illustrate temporal variation in salmon life history characters, we plotted time series of seven traits in populations for which the $\log_e$- or arcsin-transformed variances represented the among-population means, minima, and maxima (Fig. 11; Appendix 2).

Fig. 9. Effect of survival in fresh water and at sea on growth rate thresholds for sea age at maturity in female Atlantic salmon. Figures A–C illustrate changes in thresholds effected by changes in egg-to-smolt survival at low (0.0135), average (0.0740), and high (0.1740) rates of smolt-to-grilse survival. Figures D–E illustrate changes in thresholds effected by changes in smolt-to-grilse survival at low (0.25), average (0.55), and high (0.75) ratios of survival between the sea survival of 1SW versus 2SW salmon. Growth rate thresholds are defined further in the caption for Fig. 8.



The longest continuous time series of estimates of percent grilse (24 years; Western Arm Brook; Fig. 11A) exhibits remarkably low variation with estimates ranging between 95 and 100% although annual fluctuations of 20 to 30% appear to be not uncommon in other populations. Smolt-to-grilse survival, adjusted for grilse percentage as described previously, ranged from 2.1 to 12.2% for Western Arm Brook, the population for which interannual variance in survival represented the among-population average (Fig. 11B). Annual fluctuations in grilse sex ratio ranged from a low of 5% (NE Placentia River) to as much as 50% (Lomond River) with 10 to 20% being typical (Fig. 11C). For the only time series of fecundity extending more than 3 years, annual changes of 500 to 1000 eggs per female appear to be not uncommon (Fig. 11D).

Smolt age fluctuated comparatively little within populations, varying by less than 0.5 year annually within populations (Fig. 11E). Annual changes in grilse length of 2 to 3 cm appear to be typical (e.g., Western Arm Brook;

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Fig. 10. Effect of fecundity on growth rate thresholds for sea age at maturity in female Atlantic salmon at low (0.0135), average (0.0740), and high (0.1740) rates of smolt-to-grilse survival (A–C). Growth rate thresholds are defined further in the caption for Fig. 8.

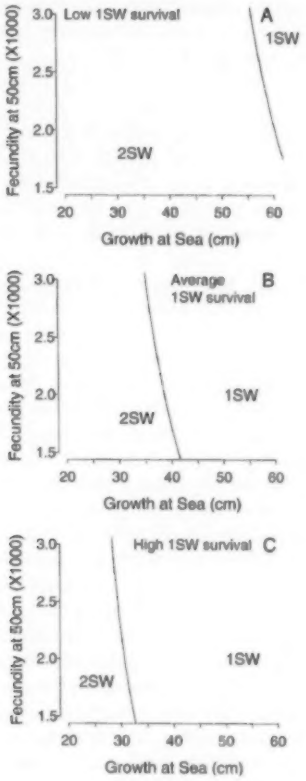

Fig. 11F) although for some populations (e.g., Conne River) this variable is remarkably constant. Annual fluctuations in smolt length are typically less than 1 cm, as indicated by salmon from Norway's River Alta (Fig. 11G).

Temporal variation in life history characters was generally uncorrelated with life history trait means of other characters. A notable exception was a negative association between sea age at maturity and temporal variance in survival at sea for 15 populations throughout the species' geographical range ($r = -0.51$, $p = 0.025$).

Discussion

Our initial postulate that life history variation in Atlantic salmon is matched by few vertebrates seems an appropriate characterization of the life history data available for this species. There are sufficient data on Atlantic salmon to construct an empirical framework against which life history responses to changes in growth rate and mortality can be predicted. What cannot as yet be predicted with confidence is the rate at which such changes might occur. This is a question of quantitative genetics and phenotypic plasticity, and the answer(s) depend upon the amount of heritable variation in life history traits, the sign and magnitude of genetic correlations among traits, the existence of reaction norms, and temporal variation in the environment (Charlesworth 1990; Roff 1997). Based on previous research (see also Fleming 1998; Marschall et al. 1998; Metcalfe 1998), the spatial and temporal data presented here, and our optimality modelling of sea age at maturity, there are sufficient data from which some general conclusions regarding the effects of growth and survival on Atlantic life history can be drawn. Following a discussion of these below, we suggest areas of research, for which there is comparatively little information, upon which future work on Atlantic salmon life history might focus.

Influence of growth rate on seaward migration and maturity as parr

The negative association between parr growth rate and smolt age (Fig. 7A) is consistent with individual and population studies in the wild and in the laboratory. The hypothesis that increased growth rate in fresh water leads to decreased age at smoltification was first proposed by Dahl (1910). He postulated that the reduction in length of growing season was responsible for the increase in smolt age with latitude in Norwegian populations. Power (1981) also found smolt age in Québec, Newfoundland, and Labrador populations to be negatively associated with length of growing season. Metcalfe and Thorpe (1990) have shown that this negative association persists throughout the geographical range of Atlantic salmon and that more than 82% of the among-population variation in smolt age can be explained by a temperature- and photoperiod-based metric of growth rate in freshwater. At the individual level, Menzies (1927) observed that the oldest smolts in two Scottish populations tended to be those having the slowest growth rates as parr. This negative association between parr growth rate and smolt age, further noted by Jones (1959) and Shearer (1972), has been documented repeatedly in the laboratory (e.g., Thorpe 1977; Thorpe and Morgan 1980; Saunders et al. 1982; see Thorpe 1986 and Saunders 1986).

How might increased growth rate be related to the fitness benefits of early maturity? Rapid growth during pre-reproductive ages reduces the time required to attain a size at which reproduction is possible. By shortening this period of time, an individual increases its probability of surviving to reproduce. For anadromous salmon, the sooner an individual migrates to sea, the sooner it reaches a size at which it can reproduce. This provides one explanation for the negative association between parr growth rate and smolt age among Atlantic salmon populations. Similarly, increased incidence of maturity with increased growth rate can be interpreted as an adaptive response by male parr (Hutchings and Myers 1994; Thorpe et al. 1997; Metcalfe 1998). Such a maturation response appears not to be adaptive for female parr, presumably because the fitness benefit of increased pre-reproductive survival does not outweigh the fitness cost of the low fecundity effected by small body size.

Fitness trade-offs between early and delayed maturity at sea

Previous support for the hypothesis that growth rate at sea influences sea age at maturity has been equivocal. In his review, Gardner (1976) found evidence of both positive and

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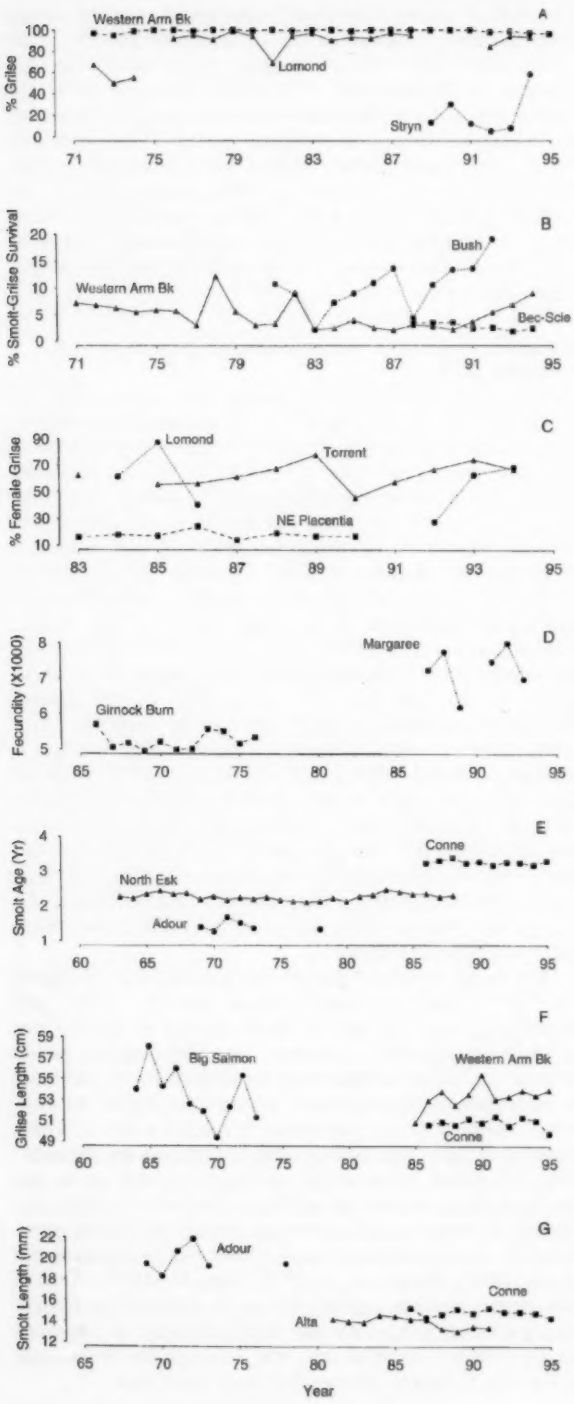

Fig. 11. Temporal variation in Atlantic salmon life history characters. The variances of proportional data (i.e., survival, percentage grilse, grilse sex ratio) have been calculated from original proportions, p, transformed as $\arcsin(p^{1/2})$. Variances of non-proportional data have been calculated from $\log_e$-transformations of the original data. Plotted time series are those that approximate the among-population means (▲—▲), minima (■ – – – ■), and maxima (● - - - ●).

negative associations between growth at sea and time spent at sea, concluding that, "it is certain there is no causal or universal relationship between growth rate ... in the sea, and the age at eventual return to fresh water" (Gardner 1976:320). Similar to our pattern (Fig. 7B), Schaffer and Elson (1975) previously documented a positive association between growth at sea and age at maturity for 14 North American populations, although their observation was supported neither by a re-analysis of the same data nor by an analysis of an expanded population data set (Myers and Hutchings 1987).

Our modelling of growth rate thresholds provides an empirical framework against which changes in sea age at maturity effected by changes in growth rate at sea can be predicted. For a given age-specific schedule of survival and fecundity, i.e., within a single population, optimal sea age at maturity is predicted to either decline or remain constant with increases in growth rate at sea (Figs. 8–10); delayed maturity appears not to be favoured by increased growth rate, all else being equal. The conclusion that earlier age at maturity is an adaptive response to increased growth rate at sea is consistent with theory (Roff 1992; Stearns 1992; Hutchings 1993, 1996) and with life history patterns observed in Atlantic salmon (e.g., Friedland and Haas 1996) and other salmonids (e.g., Hutchings 1996, 1997).

For a given growth rate at sea, our modelling suggests that uncorrelated changes to single life history characters will often have no effect on sea age at maturity. However, when an individual's growth at sea is encompassed by the range of growth rates within which changes to sea age at maturity are predicted to be favoured by selection, uncorrelated changes to single traits influence optimal age at maturity. Early maturity (i.e., maturation as a 1SW rather than a 2SW salmon) is favoured by increases in smolt length, fecundity, survival in fresh water or at sea, and survival of grilse relative to that of 2SW salmon (Figs. 8–10). Delayed maturity is favoured by reductions in smolt size, fecundity, and survival, but by increases in smolt age.

The fitness simulations may provide some insight into the causal basis for regional differences in Atlantic salmon life history. For example, compared to Newfoundland populations, European salmon grow rapidly at sea but spend almost twice as much time in the marine environment before spawning. According to the life history simulations, such an association between growth rate and sea age at maturity is adaptive only when smolt-to-grilse survival at sea, and secondarily egg-to-smolt survival, is low. At the other extreme, the observed associations among smolt age, smolt length, growth at sea, and sea age at maturity for Newfoundland populations suggest that survival at sea, and secondarily survival in freshwater, is comparatively high.

Does age at maturity covary with temporal variation in survival?

We documented a negative association between sea age at maturity and temporal variance in smolt-to-grilse survival at sea. One implicit assumption of our analysis was that varia-

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tion in survival from the smolt to the grilse stages accurately reflected variation in survival after the grilse stage. This assumption appears reasonable, given the significantly positive correlation that exists between the variances in smolt-to-grilse and smolt-to-2SW survival probabilities for salmon in the Rivers Vesturdalsa, Bush, Imsa, and North Esk ($r = 0.99$, $p = 0.003$; ICES 1994*a*).

Although life history theory provides no clear prediction of how variation in survival at potentially reproductive ages should influence age at maturity (Charlesworth 1994), we suggest that as variation in smolt-to-grilse survival increases, so does the uncertainty associated with the probability of surviving two or more winters at sea. In environments where this uncertainty is high, selection may act against genotypes that delay maturity by prolonging the time spent at sea. This might account for the negative association between sea age at maturity and variance in smolt-to-grilse survival observed here.

Future research

Although addressed indirectly by the fitness simulations, we did not examine genotype-by-environment interactions in Atlantic salmon life history. Adaptive phenotypic plasticity, via selection for norms of reaction, provides one means by which genetically based life history responses to environmental change can be effected (Bradshaw 1965; Via and Lande 1985; Stearns and Koella 1986; Hutchings 1996; Roff 1998). Herein lies one of the gaps in Atlantic salmon research. There is a need for studies that focus on the underlying basis for life history change in Atlantic salmon. Are population changes in life history, e.g., sea age at maturity, or incidence of male parr maturity, generally effected by changes in gene frequencies, a comparatively slow process occurring across generations, or by phenotypic alteration along norms of reaction, a comparatively rapid response occurring within a single generation? Questions that future research might address include: Do reaction norms, such as the predicted growth rate thresholds for male parr maturity and female sea age at maturity, exist in Atlantic salmon? If so, how do the shapes of the reaction norms differ among populations and at different spatial scales? How much additive genetic variance, and thus potential for selection, exists for the shapes of such norms of reaction? Answers to these questions would provide guidance in predicting the rate and direction of life history responses to environmental influences on growth rate and survival.

A second deficiency in our knowledge of Atlantic salmon life history concerns male age at maturity, specifically the demographic and genetic consequences of male parr reproduction. Despite the considerable laboratory (see Metcalfe 1998) and theoretical (Leonardsson and Lundberg 1986; Myers 1986; Hutchings and Myers 1994) interest in proximate and evolutionary mechanisms of male parr maturity, the demographic consequences of early male reproduction has received remarkably little attention, being limited to Myers' (1994) estimate that the increased mortality and delayed age at smoltification experienced by post-reproductive male parr may be responsible for the loss of 60% of the anadromous male salmon production in some populations. How do changes in survival and growth rate at sea influence the incidence of male parr maturity (see also Marschall et al. 1998)? What are the consequences of male parr maturity to estimates of spawning requirements in Atlantic salmon populations? And, to address an issue that has received no attention in the literature, what are the genetic and ecological consequences of male parr maturity to estimates of effective and minimum viable population sizes?

A third area of life history research that merits study concerns the ecological and evolutionary mechanisms permitting the maintenance of anadromous and nonanadromous populations of Atlantic salmon in systems in which physical barriers to seaward migration are absent. Although it has received comparatively little attention (e.g., Hutchings 1986), the study of coexisting life history polymorphisms in Atlantic salmon seems likely to bear the informative fruits borne by research on resource-based polymorphisms in threespine sticklebacks, *Gasterosteus aculeatus*, (Schluter 1996) and Arctic char (Skúlason et al. 1998).

Thus, be it from an ecological, evolutionary, conservation, or harvesting perspective, we anticipate significant contributions to science from Atlantic salmon life history research that focuses upon reaction norms for age at maturity, demographic and genetic consequences of male parr maturation, and the evolutionary and ecological mechanisms that permit coexistence of anadromous and nonanadromous life history polymorphisms.

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Appendix 1.

Table A1. Atlantic salmon life history data from unpublished and published sources used in the present study.

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
England	Avon	11.8	1.11											Harris (1973)
England	Dart		2.04											Nott (1973)
England	Tees	14.6	2.07											Harris (1973)
England	Wye		2.01											Harris (1973)
Finland	Simojoki		2.7											Toivonen and Jutila (1982)
France	Adour	19.3	1.42	1.51	65.6	79.9	94.2	0.063					193	Bousquet and Marty (1987)
France	Aulne		1.45		57	77		0.015						Baglinière et al. (1987)
France	Blavet				63	75		0.174	0.42					Baglinière et al. (1987); Prévost and Porcher (1996)
France	Bresle	16.2	1.23	1.21				0.8			0.1287		162	Fournel et al. (1987); ICES (1994*b*)
France	Ellé		1.42		65	75.7		0.091	0.42					Prévost and Porcher (1996); Baglinière et al. (1987)
France	Elorn		1.57		64	75		0.087	0.466					Prévost and Porcher (1996); Prouzet and Gaignon (1982, 1985); Baglinière et al. (1987)
France	Léguer		1.27		63.4	78.7		0.032					187	Baglinière et al. (1987)
France	Nivelle	18.7	1.04	1.17	67.7			0.84	0.54		0.0617		146.6	Bousquet and Marty (1987); Dumas (1979); ICES (1994*a*)
France	Oir								0.32	0.00292				Baglinière et al. (1993); ICES (1994*a*,*b*); Prévost and Porcher (1996)
France	Scorff		1.31		62.8	77.4		0.166	0.422			0.65		Baglinière and Champigneulle (1986); Baglinière et al. (1987, 1994); Prévost and Porcher (1996)
France	Selune		1.22		63	76.4		0.263	0.28					Baglinière et al. (1987, 1993)
Iceland	Álftá							0.74						Scarnecchia (1983)
Iceland	Andakílsá							0.84						Scarnecchia (1983)
Iceland	Austurá							0.39						Scarnecchia (1983)
Iceland	Bakkaá							0.465						Scarnecchia (1983)
Iceland	Blanda							0.255						Scarnecchia (1983)
Iceland	Breiddalsá							0.81						Scarnecchia (1983)
Iceland	Bruará							0.375						Scarnecchia (1983)
Iceland	Brynjudalsá							0.88						Scarnecchia (1983)
Iceland	Bugda							0.81						Scarnecchia (1983)
Iceland	Deildará							0.425						Scarnecchia (1983)
Iceland	Eldvatn							0.875						Scarnecchia (1983)
Iceland	Ellidaár	12.5	3.05	1.39				0.61			0.1754			Scarnecchia (1983); Gudjónsson (1978); ICES (1994*a*)
Iceland	Fáskrúd							0.705						Scarnecchia (1983)
Iceland	Fljótaá							0.54						Scarnecchia (1983)
Iceland	Flekkudalsá							0.785						Scarnecchia (1983)
Iceland	Flókadalsá							0.895						Scarnecchia (1983)
Iceland	Fnjóská							0.35						Scarnecchia (1983)
Iceland	Fossá í Laxárdal							0.455						Scarnecchia (1983)

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Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Iceland	Fródá							0.72						Scarnecchia (1983)
Iceland	Geirlandsá							0.71						Scarnecchia (1983)
Iceland	Gljúfurá							0.945						Scarnecchia (1983)
Iceland	Grímsá		2.94	1.5				0.5						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Hafralónsá							0.285						Scarnecchia (1983)
Iceland	Haffjardará							0.63						Scarnecchia (1983)
Iceland	Haukadalsá							0.645						Scarnecchia (1983)
Iceland	Hítará							0.67						Scarnecchia (1983)
Iceland	Hofsá í Vesturdal							0.43						Scarnecchia (1983)
Iceland	Hölkná							0.38						Scarnecchia (1983)
Iceland	Hördudalsá							0.745						Scarnecchia (1983)
Iceland	Hrófá							0.515						Scarnecchia (1983)
Iceland	Hrútafjardará/Siká							0.44						Scarnecchia (1983)
Iceland	Húseyjarkvísl							0.835						Scarnecchia (1983)
Iceland	Hvannadalsá							0.515						Scarnecchia (1983)
Iceland	Hvítá í Borgarf		3.03	1.62				0.41						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Hvolsá/Stadarh							0.79						Scarnecchia (1983)
Iceland	Ísafjardadá							0.625						Scarnecchia (1983)
Iceland	Krossá á Skardsst							0.795						Scarnecchia (1983)
Iceland	Langá							0.84						Scarnecchia (1983)
Iceland	Langadalsá							0.415						Scarnecchia (1983)
Iceland	Laugardalsá							0.645						Scarnecchia (1983)
Iceland	Laxá á Ásum							0.705						Scarnecchia (1983)
Iceland	Laxá á Skögst							0.71						Scarnecchia (1983)
Iceland	Laxá á Hrútafirdi							0.51						Scarnecchia (1983)
Iceland	Laxá í Adaldal							0.29						Scarnecchia (1983)
Iceland	Laxá í Adaldalur		3.05	1.64				0.368						Gudjónsson (1978)
Iceland	Laxá í Kjós		2.99	1.68				0.319						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Laxá í Lsveit							0.745						Scarnecchia (1983)
Iceland	Laxá-Ytri							0.58						Scarnecchia (1983)
Iceland	Leirá							0.93						Scarnecchia (1983)
Iceland	Leirvogsá							0.855						Scarnecchia (1983)
Iceland	Midá í Dölum							0.715						Scarnecchia (1983)
Iceland	Midfjardará		3.39	1.64				0.356						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Midfjardará/Kverká							0.43						Scarnecchia (1983)
Iceland	Nordurá		3	1.41				0.594						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Núpsá							0.48						Scarnecchia (1983)
Iceland	Olfusá	12.3	2.95	1.35				0.653						Gudjónsson (1978)
Iceland	Ormarsá							0.4						Scarnecchia (1983)
Iceland	Reykjadalsá							0.77						Scarnecchia (1983)
Iceland	Sæmundará							0.33						Scarnecchia (1983)
Iceland	Sandá							0.38						Scarnecchia (1983)
Iceland	Selá. Stfirdi							0.595						Scarnecchia (1983)
Iceland	Selá í Vopnafirdi							0.5						Scarnecchia (1983)
Iceland	Skjálfandafljót							0.44						Scarnecchia (1983)

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Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Iceland	Sog		2.86	1.44				0.591						Gudjónsson (1978)
Iceland	Sogid							0.66						Scarnecchia (1983)
Iceland	Stóra-Laxá							0.385						Scarnecchia (1983)
Iceland	Straumfjardará							0.585						Scarnecchia (1983)
Iceland	Svalbardsá							0.365						Scarnecchia (1983)
Iceland	Svartá							0.41						Scarnecchia (1983)
Iceland	Thjórsá							0.34						Scarnecchia (1983)
Iceland	Thverá		3.06	1.4				0.597						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Úlfarsá	12.6						0.93						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Vatnsdalsá							0.445						Scarnecchia (1983)
Iceland	Vesturá							0.49						Scarnecchia (1983)
Iceland	Vesturdalsá							0.555			0.0342			Scarnecchia (1983); ICES !994*a*)
Iceland	Vídidalsá		3.04	1.48				0.518						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Vididalsá/Fitjaá							0.345						Scarnecchia (1983)
Iceland	Vikurá							0.375						Scarnecchia (1983)
Ireland	Burrishoole	12.1	2.24							0.0052	0.0724			ICES (1994*a*,*b*); Harris (1973); Kennedy and Crozier (1993)
Ireland	Bush	15.2		1.15				0.88		0.0119	0.0932			ICES (1994*a*,*b*); Kennedy and Crozier (1993)
Ireland	Corrib	13.4	1.75	1.11				0.89			0.0266			Brown (1988)
Ireland	Foyle				63.7									Went and Twomey (1971)
Ireland	Moy				60									Went and Twomey (1971)
Ireland	Owenduff		2.06											Harris (1973)
Labrador	Forteau		4.09	1.03	54.2	72.9		0.97	0.645					Lowe and Mullins (1996); Myers and Hutchings (1987)
Labrador	Pinware		4.2	1.16	53.2	74.3		0.84	0.372					Myers and Hutchings (1987)
Labrador	Eagle			1.03	54.4	74.7		0.97						Myers and Hutchings (1987)
Labrador	Sandhill	16	4.44	1.2	53.9	73.4	79.2	0.89			0.0815			Myers and Hutchings (1987); Power (1981); Reddin et al. (1996); Chadwick (1988)
Maritimes	Big Salmon	13.9	2.6	1.1	53.2	70.8		0.445	0.654	0.0017	0.1461			Jessop (1986); Ritter (1989)
Maritimes	Bouctouche		2.69						0.12					Atkinson and Chaput (1996)
Maritimes	East (Pictou)				55.6			0.27	0.05					Claytor et al. (1995*a*)
Maritimes	LaHave		2.17	1.29	53.6	72.5		0.71						Amiro et al. (1996, 1998); Cutting and Jefferson (1986); Myers and Hutchings (1987)
Maritimes	Liscomb			1.08	52.3	72.4	91.7	0.92						Myers and Hutchings (1987)
Maritimes	Margaree		2.42	1.36	53.5	71.1	81.7	0.59	0.11			0.75	85.8	Claytor et al. (1995*b*); Myers et al. (1986); Myers and Hutchings (1987)
Maritimes	Medway		2.58	1.24										Ritter (1974)
Maritimes	Miramichi	12.8	2.8	1.29	55.3	73.4	86.9	0.75	0.24	0.0047	0.1410	0.605	93.9	Chaput et al. (1996, 1998); Cunjak and Therrien (1998); Moore et al. (1995); Myers et al. (1986)
Maritimes	Nepisiguit		2.15						0.178					Locke and Mowbray (1996)
Maritimes	North		3.28	1.95	54.6	72.3		0.05						Myers and Hutchings (1987); Ritter (1974)
Maritimes	Philip			2.05	56.6	74.4	86.7	0.39						Claytor et al. (1995*a*); Myers and Hutchings (1987)

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Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Maritimes	Pollett		2.1							0.0198				Elson (1975)
Maritimes	Restigouche		2.82	1.67	52	76	92	0.39	0.02			0.22	82	Locke et al. (1996); Myers et al. (1986); Myers and Hutchings (1987)
Maritimes	Richibucto		2.74											Atkinson et al. (1995)
Maritimes	Saint John		2.54	1.42	56.3	78		0.55	0.144					Marshall and Jones (1996); Myers and Hutchings (1987)
Maritimes	South (Antig)				54.4				0.03					Claytor et al. (1995*a*)
Maritimes	St. Marys			1.24	54	74.9	91.1	0.76						Myers and Hutchings (1987)
Maritimes	Tabusintac		2.8											Atkinson and Hooper (1995)
Maritimes	West (Antig)							0.38						Claytor et al. (1995)
Newfoundland	Bay de l'Eau											0.724	73.1	Myers et al. (1986)
Newfoundland	Beaver	13.2	3											O'Connell and Ash (1993)
Newfoundland	Biscay Bay		3.1	1.05	52.9				0.75					O'Connell et al. (1996*a*)
Newfoundland	Branch	15.8	3.1											Chadwick et al. (1986)
Newfoundland	Burlington	15.1	3.6											Chadwick et al. (1986)
Newfoundland	Cambellton	17.7	3.5	1.05	52.5			0.95	0.763					Dempson et al. (1998*a*); O'Connell et al. (1996*a*)
Newfoundland	Champney's	15.5	3.4											Chadwick et al. (1986)
Newfoundland	Come-By-Chance											0.786	72.2	Myers et al. (1986)
Newfoundland	Conne	14.8	3.28	1.06	50.7	68.3		0.94	0.78		0.0578			Dempson et al. (1998*a*,*b*)
Newfoundland	East	13.6	4											Chadwick et al. (1986)
Newfoundland	Exploits			1.1	52	75.6		0.9						Bourgeois et al. (1996); Myers and Hutchings (1987)
Newfoundland	Farmers	16.6	3.1											Chadwick et al. (1986)
Newfoundland	Fischells	14	2.6						0.587					O'Connell and Ash (1993)
Newfoundland	Gambo	16.7	3											Chadwick et al. (1986)
Newfoundland	Gander	15.7	3.7	1.09	53.7			0.9	0.76					Dempson et al. (1998*a*); O'Connell et al. (1996*b*)
Newfoundland	Garia	15.7	2.9											Chadwick et al. (1986)
Newfoundland	Harry's		3.4	1.02	50.4	71.4		0.98	0.621					Mullins et al. (1996)
Newfoundland	Highlands	13.1	2.9	1.36	53.3	73.4		0.36				0.55	82.7	Myers et al. (1986); Myers and Hutchings (1987); O'Connell et al. (1996*a*)
Newfoundland	Humber		3.8	1.13	55	73.5	86.5	0.92						Mullins and Reddin (1996); Myers and Hutchings (1987); Power (1981)
Newfoundland	Hunt			1.75	57.8	76.6								Myers and Hutchings (1987)
Newfoundland	Indian Bay	16.7	3.3											O'Connell and Ash (1993)
Newfoundland	Little Bk Pds	17.4	3.1											Chadwick et al. (1986)
Newfoundland	Little Codroy	15	2.66	1.48	54.1	75.1	89.6	0.6	0.411	0.0293	0.0135	0.715	85.9	Murray (1968); Myers et al. (1986); Myers and Hutchings (1987)
Newfoundland	Lomond		2.86	1.14	52.4	70.7		0.86	0.55			0.486	72.7	Myers et al. (1986); Myers and Hutchings (1987); O'Connell et al. (1996*a*)
Newfoundland	Middle Bk	17.1	3.47	1.03	53.1			0.97	0.79					Dempson et al. (1998*a*); O'Connell and Ash (1993); O'Connell et al. (1996*a*)
Newfoundland	NE Placentia	13.9	2.88	1.08	52.9			0.92	0.91					Dempson et al. (1998*a*); O'Connell and Ash 1993); O'Connell et al. (1996*a*)

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Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Newfoundland	NE Trepassey	15.4	3.67	1.18				0.82			0.0622			Dempson et al. (1998*a*)
Newfoundland	North Hr	15.1	3.2	1.22	55.1	76.3		0.78				0.118	84.3	Myers et al. (1986); Myers and Hutchings (1987); O'Connell and Ash (1993)
Newfoundland	Northwest	17.2	4									0.952	90.5	Chadwick et al. (1986); Myers et al. (1986)
Newfoundland	Pipers Hole	16.4	3.4											Chadwick et al. (1986)
Newfoundland	Ragged Hr	17.6	3.5											O'Connell and Ash (1993)
Newfoundland	Red Harbour	14.7	3.2											Chadwick et al. (1986)
Newfoundland	Renews	17.8	2.7											Chadwick et al. (1986)
Newfoundland	River of Pds	16.2	3.3											O'Connell and Ash (1993)
Newfoundland	Riverhead	16	3.4											Chadwick et al. (1986)
Newfoundland	Robinsons	13.5	2.9						0.551					Mullins et al. (1996); O'Connell and Ash (1993)
Newfoundland	Salmonier	16	3.1											Chadwick et al. (1986)
Newfoundland	Sops Arm	13	4.1											Chadwick et al. (1986)
Newfoundland	Southwest	13.4	3											Chadwick et al. (1986)
Newfoundland	St. Geneviev	17	4.2											Chadwick et al. (1986)
Newfoundland	Taylor Bay	17.5	3.3											Chadwick et al. (1986)
Newfoundland	Terra Nova	14.9	3.44	1.21	52.3			0.79	0.74					Dempson et al. (1998*a*); O'Connell et al. (1996*a*);
Newfoundland	Terrenceville	13.9	3.3											Chadwick et al. (1986)
Newfoundland	Torrent		3.17	1.07	52.7			0.93	0.647					O'Connell et al. (1996*a*)
Newfoundland	Trouty	16.7	3.2											Chadwick et al. (1986)
Newfoundland	Wst Arm Bk	16.8	3.68	1.01	52.9			0.99	0.778	0.0167	0.0489	0.039	75.4	Myers et al. (1986); O'Connell et al. (1996*a*)
Newfoundland	Wings Bk	16.4	4	1	51							0.793	76.3	Hutchings (1985, 1986); Myers et al. (1986)
Norway	Altaelva	13.5	4.2	2.15				0.423	0.056					Lund et al. (1989); Saksgård et al. (1992)
Norway	Årøelva	14.8	3.1	2.64		89.3	104.8						86.3	Huitfeldt-Kaas (1946)
Norway	Beiarelva	13.6	5.4										52.4	Jensen and Johnsen (1985); Økland et al. (1993)
Norway	Blomo		3.16	1.69										Dahl (1937)
Norway	Bondalselv				57.54	80.25								Jonsson et al. (1991)
Norway	Drammenselv				66.27	90.32								Jonnson et al. (1991)
Norway	Eira	12.1	2.88	2.53		83.2	104.1						81	Huitfeldt-Kaas (1946)
Norway	Etneelv				62.36	77.83								Jonsson et al. (1991)
Norway	Figgenelva	11.7	2.28	1.47	58.3	77.1							84	Huitfeldt-Kaas (1946)
Norway	Figgjo				59.31	75.95					0.0399			Jonsson et al. (1991); Friedland et al. (unpublished data)
Norway	Håelva	12.5	2.47	1.32	60.2	80							89	Huitfeldt-Kaas (1946); Jonsson et al. (1991)
Norway	Imsa	15.4	1.95	1.19	61.29	82.36	90.6	0.83			0.0357			ICES (1994*a*); Jonsson et al. (1991, 1998)
Norway	Kristiansand		2.96	1.63										Dahl (1937)
Norway	Lærdalselva	11.9	2.82	2.03	67.96	89.26	98.7	0.12					82	Huitfeldt-Kaas (1946); Jonsson et al. (1991); Lund et al. (1989); Økland et al. (1993)
Norway	Loneelv				55.41									Jonsson et al. (1991)
Norway	Målselva	14.5	3.66	1.72	62.5			0.47	0.039					Kristoffersen and Staldvik (1996)
Norway	Mandalselva	13.3	2.82	1.13	54	79.3							85	Huitfeldt-Kaas (1946)
Norway	Moltuen		3.66	1.72										Dahl (1937)

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Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Norway	Namsen	11.9	2.67	2.13	58.49	86.75	100.24	0.27	0.497				80	Huitfeldt-Kaas (1946); Jonsson et al. (1991); Lund et al. (1989)
Norway	Nummedals	10.5	2.47	1.91	65.4	84.5	101.7						72	Huitfeldt-Kaas (1946); Jonsson et al. (1991)
Norway	Ogna	13.2	2.65	1.24	54.6	78.6							88	Huitfeldt-Kaas (1946)
Norway	Opo				59.04	81.69	99.12							Jonsson et al. (1991)
Norway	Orkla	11.4	2.82	2.16	56.8	81.6	98.7						78	Huitfeldt-Kaas (1946)
Norway	Ørstaelv				56.92									Jonsson et al. (1991)
Norway	Otra	12.8	2.63	2.09	60.1	86.8	107.8						86	Huitfeldt-Kaas (1946)
Norway	Ranaelv				60.85	80.04								Jonsson et al. (1991)
Norway	Repparfjord			1.32				0.77						Lund et al. (1989)
Norway	Sandvikselv				64.21	83.49								Jonsson et al. (1991); Økland et al. (1993)
Norway	Saltdalselva	14.3	4.42											Jensen (1995); Økland et al. (1993)
Norway	Stjørdalselv				63.24	86.15								Jonsson et al. (1991)
Norway	Stryneelva	13.7	2.77	2.48				0.2						Jensen (1995); Lund et al. (1989)
Norway	Tana	13.3	3.11	2.53		78.7	94.5						87	Huitfeldt-Kaas (1946)
Norway	Tengselva	14.1	2.92	1.7	60.8	75.8							93	Huitfeldt-Kaas (1946)
Norway	Tovdalselva	13	2.72	1.32	52.8	76.1							87	Huitfeldt-Kaas (1946)
Norway	Varhaugelva	12.1	2.73	1	49.3								86	Huitfeldt-Kaas (1946)
Norway	Vefsna				59.34	85.48	94.31							Jonsson et al. (1991)
Norway	Vosso	14	2.88	2.54			107.3						90	Huitfeldt-Kaas (1946)
Québec	Bec-Scie		2.97	1.52						0.0156	0.0283			Caron (1992, 1996); Caron and Bolduc (1991)
Québec	Bouleau	13.1	3.14	1.57	50.6	74.6		0.43				0.13	83.6	Randall and Power (1979)
Québec	Cap-Chat			2.16	56.3	78.9	93.4	0.13						Myers and Hutchings (1987)
Québec	Cascapédia	13.9	3.30			77.7								Power (1981)
Québec	Corneille		3.02	1.71	53.3	70.0		0.13	0			0.383	98.9	Bielak and Power (1986). Myers et al. (1986); Myers and Hutchings (1987); Power (1981)
Québec	Etamamiou		3.66	1.23										Bielak and Power (1986)
Québec	George	21.5	5.85	1.95	56.1	78.7		0.05	0.20					Power (1969)
Québec	Godbout		3.36	1.67				0.82	0.02					Bielak and Power (1986)
Québec	Grande Rivière			1.97	54.9	74.4	90.9	0.12						Myers and Hutchings (1987)
Québec	Grand Trinite		3.07	1.1										Bielak and Power (1986)
Québec	Gros Mecatina		3.43	1.08										Bielak and Power (1986)
Québec	Jupiter		4.10		48.5	70.2								Power (1981)
Québec	Koksoak	20.6	5.60	1.53	62.3	80.3		0.47	0				70.0	Power (1969); Robitaille et al. (1984, 1986)
Québec	Laval		2.88	1.77										Bielak and Power (1986)
Québec	Leaf			1.88	62.4	79.7		0.12						Lee and Power (1976)
Québec	Madeleine			1.79	51.5	75.2	92.1	0.31						Myers and Hutchings (1987)
Québec	Matamek	15	3.11	1.31	52.9	72.9		0.68	0.06			0.626	85.9	Bielak and Power (1986); Gibson (1978); Myers et al. (1986); Myers and Hutchings (1987)
Québec	Matane			1.67	54.8	71.9	90.3	0.48						Myers and Hutchings (1987)
Québec	Matapédia			2.17	56.8	80	94.6	0.11						Myers and Hutchings (1987)
Québec	Mingan		3.48	1.64				0.07	0					Bielak and Power (1986)
Québec	Mistassini		3.28	1.69				0.64	0.14			0.097	76.1	Bielak and Power (1986); Myers et al. (1986)
Québec	Mitis			1.74				0.38						Côté and Beaulieu (1987)

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Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Québec	Moisie	12	3.57	2.6	48.7	74.6	90.7	0.05	0			0	63.1	Bielak and Power (1986); Myers et al. (1986); Power (1981)
Québec	Nabisipi		4.07	1.98	54.5	77.4	87.6	0.05						Bielak and Power (1986); Myers and Hutchings (1987)
Québec	Natashquan		3.95	1.33										Bielak and Power (1986)
Québec	Olomane		3.62	1.93										Bielak and Power (1986)
Québec	Pigou	15.1	2.93	1.58	53.1	72.7						0.375	96.2	Randall and Power (1979); Myers et al. (1986)
Québec	Pt. Saguenay			1.67	56.7	79.1	92.3	0.6						Myers and Hutchings (1987)
Québec	Puyjalon											0	71.3	Myers et al. (1986)
Québec	Romaine		3.1	2.08				0.02	0					Bielak and Power (1986)
Québec	Ste. Anne			2.12	56.1	80.8	95.8	0.12						Myers and Hutchings (1987)
Québec	Ste. Marguerite		3.32	1.86	52.8	75.2	90.1	0.07	0			0.167	66.3	Bielak and Power (1986); Myers et al. (1986); Myers and Hutchings (1987)
Québec	Saint-Jean	11.5	3.52	1.89	54.4	73.3	90.7	0.23	0.02	0.303	0.1282	0	54.2	Caron (1996); Caron and Bolduc (1991); Caron and Fontaine (1998); Myers et al. (1986); Myers and Hutchings (1987)
Québec	Trinité	12.1	3.00	1.29	54.2	74.7		0.59	0.08	0.0324	0.0237		80.6	Caron (1992, 1996); Caron and Bolduc (1991);Caron and Fontaine (1998); Myers and Hutchings (1987)
Québec	Grand Watchichou		3.66	1.56	53.3	70.4		0.43				0.408	89.3	Bielak and Power (1986); Myers and Hutchings (1986); Riley et al. (1984)
Québec	Whale	20.6	5.24	1.84	58.7	77.4		0.16	0.11					Power (1969)
Russia	Pizhma	14	3.9									0.1	87	Martynov et al. (1994)
Russia	Tuloma							0.53						Sharov et al. (1990)
Scotland	Almond				63.5	81.9								Thorpe et al. (1984)
Scotland	Bran	11.0	2.43											Harris (1973)
Scotland	Conon		2.62											Harris (1973)
Scotland	Dee		2.23	1.85			0.15		0.174	0.0074				Buck and Hay (1984); Harris (1973)
Scotland	Ewe		2.53											Harris (1973)
Scotland	Grimersta		2.71											Harris (1973)
Scotland	Nith		2.03											Harris (1973)
Scotland	North Esk	12.6	2.33	1.39	60.5	74.2	88.1	0.8	0.46		0.0601			ICES (1994*a*); Shearer (1992)
Scotland	Shelligan Burn		2.2	1.05										Egglishaw and Shackley (1977)
Scotland	Spey		2.30											Harris (1973)
Scotland	Tay		2.19											Harris (1973)
Scotland	Thurso	12.0	2.04											Harris (1973)
Scotland	Tweed		2.20											Mills (1989)
Spain	Cares	18.3	1.15	2.18				0.05					183	Nicieza and Braña (1993*a*,*b*); Nicieza et al. (1991); Ventura (1987)
Spain	Esva	15.7	1.18	2.06				0.06					157	Nicieza and Braña (1993*a*,*b*); Nicieza et al. (1991); Ventura (1987)
Spain	Narcea	17.6	1.2	2.22	70			0.05					176	Nicieza and Braña (1993*a*,*b*); Nicieza et al. (1991); Ventura (1987)
Spain	Sella		1.36	2.12				0.04						Ventura (1987)
Sweden	Eman		1.5											Karlström (1977)

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Table A1. (*Concluded*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Sweden	Kalix Alv		3											Karlström (1977)
Sweden	Mörrumsån		1.5											Lindroth (1977)
Sweden	Ricklean		2.7											Osterdahl (1964)
Sweden	Torne Alv		3.5											Karlström (1977)
U.S.A.	Connecticut	18.3	1.94	1.98				0.02					150	Friedland et al. (1996); Orciari et al. (1994)
U.S.A.	Dennys			2.01				0.01						Baum (1997)
U.S.A.	East Machias			1.96				0.05						Baum (1997)
U.S.A.	Machias			1.97				0.04						Baum (1997)
U.S.A.	Penobscot			1.84	55.0	72.5	87.0	0.11						Baum (1997); Friedland et al. (1996)
U.S.A.	Pleasant			1.97				0.07						Baum (1997)
U.S.A.	Narraguagus	17.7	2.22	2.00	60.0	76.0	89.0	0.02						Baum (1997)
U.S.A.	Sheepscot			1.94				0.09						Baum (1997)
U.S.A.	Dee		1.98											Harris (1973)

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Appendix 2.

Table A2. Temporal variation in Atlantic salmon life history characters. The variances of proportional data (i.e., survival, percentage grilse, grilse sex ratio) have been calculated from original proportions, p, transformed as $\arcsin(p^{1/2})$. Variances of non-proportional data have been calculated from $\log_e$- transformations of the original data.

Trait	Region	River	Number of years	Years	Variance
Smolt-to-grilse survival	Québec	St. Jean	6	89–94	0.0026
		Trinité	11	84–94	0.0020
		Bec-Scie	7	88–94	0.0004
	Newfoundland	Sandhill	4	69–72	0.0056
		NE Trepassey	8	86–93	0.0020
		Conne	8	87–94	0.0031
		Western Arm Brook	24	71–95	0.0033
		Little Codroy	7	54–61	0.0004
	Canadian Maritimes	Miramichi	4	90–93	0.0051
		Big Salmon	5	66–71	0.0204
	Iceland	Elidaar	7	75–92	0.0103
		Vesturdalsa	5	83–92	0.0036
	Ireland	Burrishoole	14	79–92	0.0030
		Bush	12	81–92	0.0066
	Scotland	North Esk	8	81–91	0.0008
	Europe	Nivelle	5	86–90	0.0122
		Bresle	4	83–86	0.0042
	Norway	Imsa	12	81–92	0.0045
Percent grilse	Québec	Trinité	13	80–92	0.0187
		Bec-Scie	9	84–92	0.0222
	Newfoundland	NE Trepassey	8	86–93	0.0052
		Conne	9	87–95	0.0012
		Western Arm Brook	24	71–95	0.0001
		Exploits	26	60–94	0.0250
		Salmon Brook	25	57–94	0.0412
		Gander	6	89–94	0.0061
		Middle Brook	17	72–94	0.0042
		Terra Nova	34	56–94	0.0306
		Biscay Bay	12	83–94	0.0037
		NE Placentia	21	71–94	0.0137
		Highlands	5	80–94	0.0156
		Humber	5	90–94	0.0066
		Lomond	19	72–94	0.0369
		Torrent	24	71–94	0.0085
	Labrador	Sandhill	5	69–94	0.0154
	Canadian Maritimes	Miramichi	25	71–95	0.0310
		Liscomb	15	80–94	0.0114
		Saint John	29	67–95	0.0222
		Magaguadavic	8	83–95	0.0119
		St. Croix	13	82–95	0.0502
	Norway	Strynelva	6	89–94	0.0534
Percent female grilse	Newfoundland	Western Arm Brook	10	85–94	0.0092
		Gander	3	92–94	0.0046
		Middle Brook	5	83–87	0.0388
		Terra Nova	5	83–87	0.0028
		NE Placentia	9	78–86	0.0017
		Lomond	6	84–94	0.0524
		Torrent	11	83–94	0.0090
	Labrador	Forteau	9	75–94	0.0204
		Pinware	8	74–93	0.0164
	Canadian Maritimes	Nepisiquit	8	83–90	0.0014
		Big Salmon	5	68–73	0.0026

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Table A2. (*Concluded*).

Trait	Region	River	Number of years	Years	Variance
Fecundity	Newfoundland	Terra Nova	3	84–86	0.0006
		Middle Brook	3	84–86	0.0006
	Canadian Maritimes	Margaree	6	87–93	0.0086
	Scotland	Girnock Burn	11	66–76	0.0022
Smolt age	Québec	Bec-Scie	9	84–92	0.0018
		Trinité	9	84–92	0.0005
	Newfoundland	Middle Brook	5	83–87	0.0014
		Terra Nova	5	83–87	0.0004
		NE Placentia	9	78–86	0.0056
		Lomond	13	78–95	0.0046
		Torrent	15	75–95	0.0017
		Western Arm Brook	25	71–95	0.0032
		Conne	10	86–95	0.0004
	Labrador	Forteau	8	78–94	0.0009
	Scotland	North Esk	26	63–88	0.0019
	Europe	Adour	6	69–78	0.0100
	Norway	Stryneelva	6	89–94	0.0018
		Saltdalselva	5	90–94	0.0010
		Altaelva	11	81–91	0.0010
Grilse length	Newfoundland	Terra Nova	5	83–87	0.0003
		NE Placentia	8	78–86	0.0003
		Torrent	11	83–94	0.0002
		Western Arm Brook	10	85–94	0.0005
		Conne	10	86–95	0.0001
	Labrador	Forteau	9	79–94	0.0002
	Canadian Maritimes	Big Salmon	10	64–73	0.0022
		LaHave	13	85–97	0.0003
		Miramichi	27	71–97	0.0009
Smolt length	Québec	St-Jean	10	88–97	0.0006
		Trinité	10	88–97	0.0005
	Newfoundland	Conne	10	86–95	0.0005
	Europe	Adour	9	69–82	0.0040
	Norway	Altaelva	11	81–91	0.0013

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A framework for understanding Atlantic salmon (*Salmo salar*) life history

Elizabeth A. Marschall, Thomas P. Quinn, Derek A. Roff, Jeffrey A. Hutchings, Neil B. Metcalfe, Tor A. Bakke, Richard L. Saunders, and N. LeRoy Poff

Abstract: We took a hierarchical approach to understanding Atlantic salmon (*Salmo salar*) life history patterns by first comparing salmonids to other teleosts, next comparing Atlantic salmon to other salmonids, and finally, mapping correlations among individual life history traits within Atlantic salmon. The combination of anadromy, large eggs, nest construction and egg burial by females, and large size at maturity differentiates salmonids from most other teleosts. Within the family Salmonidae, there is considerable variation in all traits but Atlantic salmon are generally in the middle of the range. Within Atlantic salmon, we were able to map correlations among individual life history traits, but we found that we still lacked an understanding comprehensive and quantitative enough to allow us to predict how the entire life history should respond to environmental changes. Thus, we proposed several general courses of action: (*i*) use models to synthesize complex patterns and relationships, (*ii*) collect long time series of data in individual systems, and (*iii*) design experiments to assess phenotypic plasticity and how environmental influences differ from genetic effects and constraints.

Résumé : Nous avons adopté une démarche hiérarchique pour comprendre les patrons du cycle biologique du saumon de l'Atlantique (*Salmo salar*) en comparant tout d'abord les salmonidés à d'autres téléostéens, puis le saumon atlantique à d'autres salmonidés, et enfin en cartographiant les corrélations ente les traits individuels du développement chez le saumon atlantique. La combinaison de l'anadromie, de la grande taille des oeufs, du creusement du nid et de l'enfouissement des oeufs par la femelle et de la grande taille à la maturité différencie les salmonidés de la plupart des autres téléostéens. Au sein de la famille des Salmonidae, on note une variation considérable dans tous les traits, mais le saumon atlantique se situe généralement au milieu de la fourchette. Chez le saumon atlantique, nous avons pu cartographier les corrélations entre certains traits individuels, mais nous avons constaté que notre compréhension n'était pas encore assez détaillée et quantitative pour nous permettre de prédire comment l'ensemble du cycle biologique devrait réagir aux changements environnementaux. Nous proposons en conséquence diverses approches générales (*i*) avoir recours à des modèles pour faire la synthèse des patrons et relations complexes, (*ii*) recueillir des séries de données dans des systèmes individuels sur une longue période, (*iii*) concevoir des expériences visant à évaluer la plasticité phénotypique et la façon dont les influences environnementales diffèrent des effets et contraintes d'ordre génétique.

[Traduit par la Rédaction]

Introduction

Atlantic salmon, *Salmo salar*, have been the subject of much research owing to their great commercial and recreational importance on two continents, a very large Atlantic salmon aquaculture industry, and their suitability as models for studies of behavior, ecology, and evolution, among other disciplines. However, we still do not fully understand what drives patterns of variation in their life histories. Researchers have concentrated their studies on specific stages of Atlantic salmon life history or on life history patterns in specific geographic locations. Our objective is to draw together research from these disparate fields to construct a framework within which we can begin to develop a broader understanding of Atlantic salmon life history.

A first step in understanding what drives life history patterns in any taxon is to separate patterns and traits that

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E.A. Marschall.[1] Aquatic Ecology Laboratory, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, OH 43212–1156, U.S.A.
T.P. Quinn. School of Fisheries, University of Washington, Seattle, WA 98195, U.S.A.
D.A. Roff. Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada.
J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.
N.B. Metcalfe. Division of Environmental and Evolutionary Biology, Glasgow University, Glasgow G12 8QQ, U.K.
T.A. Bakke. Zoological Museum, University of Oslo, 0562 Oslo, Norway.
R.L. Saunders. Fisheries and Oceans Canada, Biological Station, St. Andrews, NB E0G 2X0, Canada.
N. LeRoy Poff. Biology Department, Colorado State University, Fort Collins, CO 80523, U.S.A.

[1]Author to whom all correspondence should be addressed. e-mail: marschall.2@osu.edu

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distinguish that taxon from those in related taxa. We begin by describing how salmonid life histories differ from those of other teleost fishes, then we discuss how Atlantic salmon differ from salmonids in general, and finally, we look closely at patterns of variation within Atlantic salmon. Although there are some robust correlations between individual life history traits (e.g., female size is positively correlated with egg number), we are unable to make confident predictions about how changes at one stage translate into changes more than one or two direct links away (e.g., how does a change in female size affect parr size at maturity?). Thus, we suggest avenues of research, both model-based and empirical, that will lead to greater understanding of how changes at one life stage translate to changes at other life stages. Only through this depth of understanding can we predict life history responses by Atlantic salmon to changes in their environment and to future management actions.

Life history patterns: salmonids versus other teleosts

We compared salmonid life history traits (parental care, egg size, spawning and emergence dates, age and size at maturation, anadromy, and iteroparity) to those of teleosts in general and then compared life history traits of Atlantic salmon to those of salmonids in general (regarding the genera *Salmo*, *Salvelinus* (char), and *Oncorhynchus* (Pacific salmon) as representative of the family Salmonidae). Fish in general, and salmonids in particular, are genetically variable and phenotypically flexible in their life history traits. Thus, our generalizations about salmonids have exceptions within and among groups.

Egg stage

Salmonids differ from most teleosts in several traits associated with the egg stage. Like the great majority of fishes, salmonids lay eggs rather than produce live young, though the selection (Kondolf and Wolman 1993), modification (Kondolf et al. 1993), and guarding of a nest that generally characterizes salmonids (Groot and Margolis 1991) places them in the distinct minority of fish families. Parental care is found in only about 21% of teleost families and is more common among freshwater than marine fishes (Blumer 1982; Gross and Sargent 1985). Among the fishes that practice uni-parental care, the male is more often the care-giver than the female (61%), again distinguishing salmonids, in which only the female builds and guards the nest (Gross and Sargent 1985). The burial of eggs that is characteristic of salmonids (DeVries 1997) (though lake trout, *Salvelinus namaycush*, are an exception) is an uncommon form of parental care (Blumer 1982). Most fishes that do bury their eggs have comparatively small eggs and short incubation periods (e.g., Osmeridae and Cyprinidae), the latter perhaps related to the risk of deterioration of the nest environment during a protracted period of incubation (see Peterson and Quinn 1996*a*, 1996*b* for evidence of the changes in the environment of salmon embryos during incubation).

Despite the risk of deterioration of the nest, salmonids often have long incubation periods as many species spawn in the fall and fry do not emerge until in the spring. Canadian freshwater fishes (which may be taken to represent species spawning in the same general environment as salmonids) show a bimodal distribution of spawning periods (Wootton 1984). Most spawn in the spring or early summer and a smaller number, including many salmonids and coregonids, spawn in fall or winter and incubate during the coldest months of the year. The bimodal distribution of spawning periods converges into a unimodal distribution of emergence–hatching dates, however, as virtually all North American freshwater fish larvae, including salmonids, complete yolk absorption and initiate exogenous feeding in spring–early summer.

The long incubation period typical of salmonids is associated with unusually large eggs, even among the spring-spawning species (Hutchings and Morris 1985). Egg size generally increases with body size within salmonid populations but varies among species and populations (Beacham and Murray 1993; Fleming 1996; Hutchings 1998). Fecundity of salmonids is comparatively low for their body size; most teleosts have much smaller, more numerous eggs (Elgar 1990; Winemiller and Rose 1993; Chambers and Leggett 1996). The connection between large eggs, nest construction, and a protracted incubation period is a defining feature of salmonid life histories, as embryos are maintained on endogenous food reserves for several months. During these prefeeding stages, the embryos incubate in stream or lake gravels for a period of time that is negatively correlated with water temperature (Beacham and Murray 1990). The salmonid pattern contrasts with the high egg number, small eggs, brief incubation period, and dependence on food-rich environments typical of most fish species (Hutchings and Morris 1985; Winemiller and Rose 1992, 1993). It should be noted that the coregonids (whitefish and cisco), which are close relatives of the salmonids, spawn in fall and winter but produce smaller eggs than the salmonids and also apparently do not provide parental care (Scott and Crossman 1973).

Age at maturation

Despite a great range in age at maturation, Canadian freshwater fishes exhibit a distinct size-at-maturation mode at 50–100 mm (Wootton 1984). Salmonids vary greatly in size at maturation, chiefly because of the differences in growing opportunities in streams, lakes, and marine environments. Although some populations of salmonids mature at very small sizes (e.g., brook trout, *Salvelinus fontinalis*: Hutchings 1994; landlocked Atlantic salmon: Gibson et al. 1996) and some males may mature as parr at a small size (notably Atlantic salmon, which may mature at sizes as small as 10 cm in freshwater: Fleming 1996), the family as a whole is much larger at maturation than the modal size of other freshwater fishes (Hutchings and Morris 1985). Anadromous Pacific salmonids are often 500–800 mm at the time of first spawning (Groot and Margolis 1991). The modal lifespan of Canadian freshwater fishes is 4–9 yr and in this regard the salmonids are not atypical (though lake trout and representatives of other iteroparous species can live to be quite old). Salmonids are thus large for their age, compared to freshwater fishes, in part due to their anadromous behavior and rapid growth rates at sea. This is reflected in the unusually high salmonid catch:biomass ratio sustainable in the North Pacific Ocean, relative to other

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production domains and fish species (Ware and McFarlane 1989).

Anadromy

The capacity to exploit marine food resources results from the anadromous life cycle displayed in most salmonids and this is an essential feature of the family. McDowall (1987) concluded that there are about 160 diadromous fish species, or about 0.65% of the estimated total of 24 618 fish species (Nelson 1994). Of the diadromous species, 54% are anadromous, the others being catadromous or amphidromous. Thus, anadromy is not unique to salmonids but this life history pattern makes them very unusual among fishes. Salmonids are not only anadromous but show a strong tendency to return to spawn at their natal site. Although the literature on homing in fishes is dominated by work on salmonids, it seems that some form of homing may be common among fishes in general (Quinn and Dittman 1992). Homing results in reproductive isolation of salmonid populations but straying, especially by anadromous individuals, permits gene flow among populations. Analyses of patterns of genetic diversity among fish species have indicated that freshwater fish populations are more differentiated than those of marine fishes and anadromous fishes show intermediate levels of differentiation (Gyllensten 1985; Ward et al. 1994).

Summary

Salmonids differ in many notable aspects from other fishes. However, their freshwater habitat requirements seem to be quite adaptable. The best evidence for this is the numerous successful transplants throughout the world. Populations of nonnative salmonids (especially brown trout, *Salmo trutta*; rainbow trout, *O. mykiss*; brook trout, and Atlantic salmon) have been established in all continents except Antarctica (MacCrimmon and Marshall 1968; MacCrimmon and Campbell 1969; MacCrimmon 1971; MacCrimmon and Gots 1979). The paucity of successful transplants of anadromous populations, even within the native range of the species, however, indicates that this is a highly specialized feature of their biology (McDowall 1988).

Life history patterns: Atlantic salmon versus salmonids

Spawning

Although salmonids as a group differ from most teleosts in many respects, Atlantic salmon life history patterns are generally representative of the family. They spawn in autumn–winter (Heggberget 1988), in keeping with many species but differing from others, notably rainbow trout, cutthroat trout (*Oncorhynchus clarki*), and grayling (in the related family Thymallidae) that spawn in the spring. They spawn mostly in streams, as is typical of the family (with the exception of lake trout). The mechanics of nest construction, courtship, and spawning are quite similar within the family and Atlantic salmon seem to be no exception (Groot and Margolis 1991; Fleming 1996).

Egg size

Atlantic salmon have smaller eggs for a given body size than Pacific salmon (Beacham and Murray 1993; Fleming 1996) and their fecundity is somewhat higher. Incubation time is within the range of Pacific salmon but shorter than most (days from fertilization to 50% hatching at 8°C: Atlantic salmon = 63; coho, *O. kisutch* = 63; chinook, *O. tshawytscha* = 67; chum, *O. keta* = 67; pink, *O. gorbuscha* = 72; sockeye, *O. nerka* = 77; Crisp 1988; Murray and McPhail 1988). The main source of variation within the family seems to be the slower temperature-specific incubation rate of fall-spawning compared with spring-spawning species (Brannon 1987). Leitritz and Lewis (1980) listed 41, 44, and 49 days to hatch at 10°C for brown, brook, and lake trout (fall spawners), respectively, compared with only 31 for spring-spawning rainbow trout.

Freshwater rearing habitat

Most juvenile Atlantic salmon spend their first year or more (1–8) residing in stream habitats (Metcalfe and Thorpe 1990; Gibson 1993). In this regard they are like most salmonids but unlike lacustrine species such as lake trout and sockeye salmon and species that migrate directly to sea such as pink, chum, and some populations of chinook salmon. Rearing habitat in streams varies among populations and also changes as the fish age, but Atlantic salmon parr tend to occupy territories with relatively high water velocities (see review by McCormick et al. 1998). However, some populations of Atlantic salmon rear in lakes (Berg 1985) rather than streams. Such flexibility with respect to rearing habitat is quite common within the family. Swain and Holtby (1989) documented distinct stream- and lake-rearing coho salmon populations. Most sockeye salmon populations rear in lakes but others rear in rivers or migrate directly to sea (Wood et al. 1987) and brown trout also occupy a range of freshwater habitats. Atlantic salmon are thus quite typical of the salmonids, having a "characteristic" habitat but also having populations that occupy distinctly different habitats.

Anadromy

Most Atlantic salmon are anadromous, but freshwater populations exist and males commonly mature as parr in streams (Berg 1985). The degree of anadromy displayed by Atlantic salmon is intermediate within a family that ranges from chum and pink salmon (always anadromous in their native range) to lake trout (never anadromous; Rounsefell 1958; McDowall 1988). Rounsefell (1958) considered Atlantic salmon to be less anadromous than sockeye salmon and more so than rainbow trout. One life history trait linked to anadromy is the occurrence of sexually mature male parr. Such parr are common in Atlantic salmon (Fleming 1996) but are not typical of Pacific salmon in North America. However, mature parr have long been known in some populations of chinook salmon (e.g., Snyder 1931) and are common in brown trout (Bohlin et al. 1994) and masu salmon, *O. masou* (Kato 1991; Tsiger et al. 1994).

Atlantic salmon are large at seaward migration (Hutchings 1998) comparable to steelhead trout but larger than most Pacific salmon. The marine migration patterns of Atlantic salmon most closely resemble those of steelhead trout (except the Asian coastal populations; Burgner et al. 1992), sockeye salmon, or stream-type chinook salmon (Groot and Margolis 1991). These species apparently make only limited use of estuaries, move rapidly to the open ocean, and feed

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there for a year or more. Most Atlantic salmon returning from the ocean are maturing and will spawn before migrating back to sea, unlike some salmonids which often migrate back to freshwater but do not spawn that season, such as Dolly Varden char, *Salvelinus malma* (Armstrong 1981), brown trout (Jonsson 1985), steelhead trout (Burgner et al. 1992), brown trout (Jonsson 1985), and Arctic char (Nordeng 1983). The relationship between the date of river entry and the date of spawning varies greatly, however, and in some stocks of Atlantic salmon, individuals return nearly a year before they spawn, arriving in the rivers in late autumn and not spawning until the following autumn (Berg 1964; Saunders 1981).

Anadromous Atlantic salmon are large at maturity (Hutchings 1998), exceeding all but chinook among the Pacific salmon. Although less numerous than the Pacific salmon species that use streams only for spawning (pink, sockeye, and chum), their abundance is comparable to large-bodied species that have extended rearing periods in freshwater (e.g., chinook salmon and steelhead trout). With respect to iteroparity, the life history pattern of Atlantic salmon is intermediate within the family. The five North American species of Pacific salmon are semelparous (though under certain controlled conditions chinook salmon can survive after maturation and reproduce again; Bernier et al. 1993). Atlantic salmon are iteroparous, having the capacity to spawn many times (Hutchings and Morris 1985). Populations vary considerably in iteroparity and in the proportion of annual and biennial spawners (Jonsson et al. 1991). In many Atlantic salmon populations, most anadromous individuals do not survive to spawn a second time (Fleming 1996); however, other populations are characterized by high proportions of repeat spawners (Ducharme 1969; Saunders and Schom 1985).

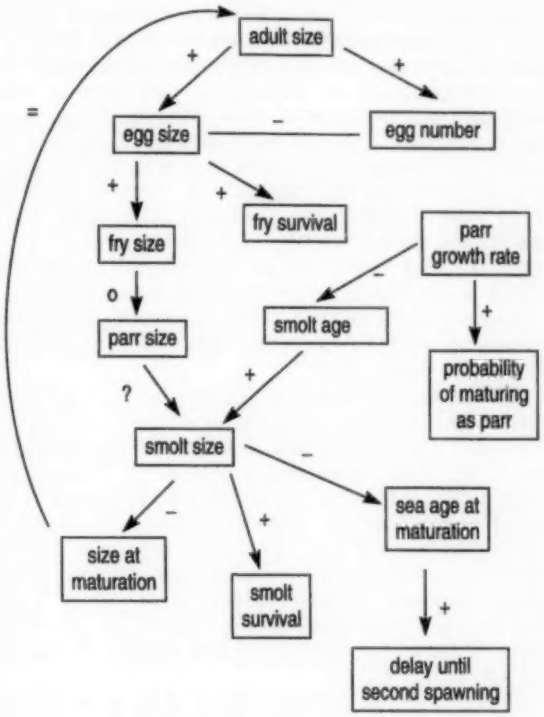
Summary

Salmonids as a family differ in many obvious respects from most fishes, notably their patterns of female parental care, burial and lengthy incubation of large eggs, rapid growth and large size at maturity associated with anadromy, and tendency toward semelparity. Despite these specialized patterns, freshwater populations have been readily transplanted around the world, hence they can successfully compete in ecosystems in which they have not evolved. Within the family, there is considerable variation in all traits but Atlantic salmon are generally in the middle of the range, not being extreme in the major traits (e.g., anadromy, iteroparity, size and age, habitat). They are thus generally suitable as a "model" for salmonid studies.

Life history patterns: correlations within Atlantic salmon

We used information from this workshop, from our own research, and from the literature to specify directions of correlations between pairs of life history traits in Atlantic salmon (Fig. 1). In some cases, we used knowledge from similar species to infer relationships in Atlantic salmon. We were interested in the relationships between life history traits within populations rather than correlations obtained from studies comparing different populations. The latter studies

Fig. 1. Directions of correlations between Atlantic salmon life history traits.



are important in showing the range of evolutionary responses but can give misleading information with respect to the within-population trajectories. For example, analysis among populations shows no significant relationship between smolt size and survival at sea (Hutchings 1998), whereas studies within a population have demonstrated a positive correlation between these two variables (e.g., Lundqvist et al. 1994).

Certain relationships are fairly predictable; for example, total ovary weight, fecundity, and egg size increase with female body size (Fleming 1996; Jonsson et al. 1996). Although this might seem to imply that egg number and egg size should be positively correlated, in fact, just the opposite is true. Egg number and egg size show a negative correlation among females of similar size (Fleming 1996). The foregoing example illustrates the need for empirical data and the care required in constructing a life history model.

As we might expect, fry size increases with egg size (Fleming 1998) and large size gives fry a survival advantage (Fig. 1). Large fry, however, do not necessarily become large parr. Rapidly growing parr smolt at a younger age (Metcalfe et al. 1989; Økland et al. 1993; Hutchings 1998; Metcalfe 1998) and a smaller size (Økland et al. 1993) than more slowly growing parr. The fastest growing parr either migrate to sea as smolts or mature as parr (Thorpe 1977, 1986; Myers et al. 1986; Bohlin et al. 1994). The incidence of smoltification and maturity among the fastest growing parr undoubtedly varies among populations and may primarily

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depend upon the age at which individuals get large enough to overcome size-biased marine mortality patterns. In Scotland, the fastest growing parr appear to be those that migrate to sea (Thorpe 1977, 1986), whereas in Canadian populations, the fastest growing males mature as parr. There is a positive correlation between growth rate (or condition factor) and likelihood of maturing as parr (Thorpe 1986; Simpson 1992; Bohlin et al. 1994; Metcalfe 1998). Smolt size is positively related to smolt survival during their migration downstream. Large smolts seem to be less vulnerable to predators (White 1957; Reitan et al. 1987; Kennedy and Greer 1988; Feltham 1990), disease (Cusack 1986; Jansen and Bakke 1993*a*, 1993*b*), and osmoregulatory stress (Bjerknes et al. 1992; Thorpe and Metcalfe 1998) than smaller smolts. Large smolts also have higher marine survival rates (Lundqvist et al. 1994). Individuals that smolt at a young age tend to be small and thus have poorer survival than larger, older smolts.

The paradoxical pattern of fast-growing parr becoming small smolts is similar to the pattern of smolt size and size at maturity. Large smolts tend to retain their size advantage over small smolts, even after a year at sea (Nicieza and Braña 1993), and tend to mature after fewer winters at sea and at smaller sizes than individuals that were smaller as smolts (Carrière and Roff 1996). Both sea-age at maturity and adult size are positively correlated with the delay until a second spawning attempt (Jonsson et al. 1991). Large (>90 cm), late-maturing (sea-age at maturity >2 yr) salmon tended to spawn biennially rather than annually in Norway (Jonsson et al. 1991).

Population or cohort density affects some of the life history parameter values described above in Atlantic salmon, particularly growth and survival during the riverine life stages. Survival from egg through fry and growth rate of parr are both inversely density dependent (Talbot 1994; Crozier and Kennedy 1995). In addition to density dependence, frequency dependence may also affect some life history traits. For example, reproductive success associated with maturing as a parr may depend on both the density and frequency of anadromous males spawning that year. When anadromous males predominate, maturing as a parr provides a way to avoid the intense competition for mates that occurs between anadromous males, although the success of this alternative strategy is of course itself frequency dependent (Hutchings and Myers 1988, 1994; Fleming 1996).

In some cases it may be tempting to use our understanding of directions of correlations among life history traits (i.e., Fig. 1) to predict how changes in one life history trait affect other life history traits, but the complexity of relationships and density or frequency dependence of rates requires a more quantitative approach. For example, we might ask how increased river temperature might affect life history characteristics such as the return age and size of Atlantic salmon (Roff and Carrière 1996). A slight increase in stream temperature produces higher growth rates (assuming adequate ration) and leads to a change in smolt size. Individuals that are large as smolts mature at smaller sizes than those that are small as smolts (see Fig. 1) and thus produce fewer eggs per female. However, these individuals that are large as smolts mature at a younger age than those that are smaller as smolts, so although they produce fewer eggs per female, they produce them in fewer years. Thus, the actual outcome for the population as a whole cannot be predicted from qualitative correlation alone.

The situation is made even more complex and the outcome more difficult to predict when we recognize that many of these life history traits are heritable and many are genetically correlated with other traits (Jonsson et al. 1991). For example, an individual's size at smoltification is at least partially determined genetically by its parents and an individual's size at age at sea is genetically correlated with its size at smoltification. We also know that size at maturity is heritable. However, genetics only partially determine these traits; the rest is influenced by environment. Thus, we have a complex set of phenotypic and genetic relationships between smolt size and size at maturity, which makes prediction of the actual response to changes in selective factors and growing conditions difficult to predict without explicit mathematical models and knowledge of the relative contribution of the environment and genetics in the expression of these life history traits.

The outcome of a sequence of events is not predictable by simple examination of the direction of correlation of pairs of traits as illustrated in the flow chart shown in Fig. 1. This analysis is not atypical of analyses of life history variation; they generally involve the interaction of several functions, frequently nonlinear, and prediction is not possible without explicit solution of the equations using numerical methods. To use our current understanding to predict outcomes of environmental changes successfully, it must be enhanced either with specific empirical information or with quantitative models. Below, we first address modeling approaches and then empirical approaches that we believe will lead to a more comprehensive understanding of Atlantic salmon life histories.

Approaches to new understanding: models

Regression models

Regression models are the simplest type of predictive models (Powers 1989). In principle they make no statement concerning the mechanism producing the regression between two traits. As an example, consider the following two regressions:

$$\text{Egg size} = c_0 + c_1(\text{Female spawner size})$$

$$\text{Female spawner size} = c_2 - c_3(\text{Smolt size})$$

where the c_0, c_1, c_2, and c_3 are fitted constants. To use these two equations for prediction we must assume that they can be chained together, i.e.,

$$\text{Egg size} = c_0 + c_1(c_2 - c_3(\text{Smolt size}))$$

which requires that the correlations be very large (>0.8), which is not typical for ecological data. Thus the separate regression of egg size on smolt size will not usually give the same constants as those from the above chaining (so, in general, the intercept will not equal $c_0 + c_1c_2$ and the slope will not equal $-c_1c_3$). Further, unless the correlations are very high, the equations cannot be algebraically manipulated to switch dependent and independent variables: thus the

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Female spawner size on egg size regression is not Female spawner size = $(1/c_1)$(Egg size $- c_0$). A further complication is that equations may be nonlinear.

Given the above considerations, the regression approach will be of limited use in constructing a general life history model. This method should be used only where there are few variables (preferably only two) and prediction is to be made only within the range of the observed data. Its strength lies in the fact that very few assumptions are made. It does, however, form the basis of the approaches described below, because almost all relationships are ultimately based on a regression analysis. The contribution that regression (linear or nonlinear) analysis plays is to establish the sign of the correlation and a range within which parameter values are constrained to lie.

Mechanistic models

In contrast to the regression approach, mechanistic models are based on an assumed functional relationship between variables; for example, the relationship between egg size and egg number might be developed based on geometric constraints. Thus we might predict that

$$\log(\text{Egg number}) = c_4 - c_5 \log(\text{Egg size})$$

where c_4 and c_5 depend on the particular geometry of the body and the egg. In practice the two constants would generally be estimated by regression. It is quite possible that the simple linear regression

$$\text{Egg number} = c_6 - c_7(\text{Egg size})$$

will fit the data equally well (i.e., there would be no significant difference in the variance accounted for by the two regressions). From the linear regression approach there is no reason to prefer one to the other. As long as predictions remain within the range of the observed data, it would not matter which model is used, but predictions outside the range could be quite different and it is at this point that the argument of function becomes important. An incorrect mechanistic argument can lead to a predictive equation that can be made to fit the data but is in fact incorrect; a good example of this is the von Bertalanffy growth function. Although the resulting model can be fitted to the data, the underlying physiology is wrong (Knight 1968) and the fit comes about simply because the equation is flexible in shape and the three parameters are not determined independently from metabolic studies but estimated from the growth data itself (Roff 1980). It is important to keep in mind the assumptions of the model components and subject them to independent tests.

Mechanistic models are very important in predicting short-term responses to changes in conditions. An example is the "proximate model" of Thorpe et al. (1998), which predicts life-history pathways in salmonids from knowledge of how an individual fish's growth performance matches genetically determined thresholds. These thresholds must be surpassed by key times of year for smolting or sexual maturation to be triggered and once these developmental processes are in train, further thresholds must be attained for the process to be completed. This simple series of switch points is capable of generating the observed wide diversity of salmonid life histories both among and within populations, because threshold values will vary among fish and both the environment and the genotype of the fish create variation in growth rates. Metcalfe (1998) illustrates how a simplified form of this approach can be used to predict demographic responses to changes in mean growth rate.

Optimality models

Mechanistic models generally make no a priori assumption about the effect of selection on model components; they are taken as fixed. In contrast, optimality models assume that some fitness measure is maximized. As a consequence, evolution will sculpt a suite of characteristics that maximizes fitness. The central assumption of optimality models is that there are trade-offs that constrain the range of possible combinations. We can consider egg number and egg size to constitute a trade-off, with some limitation of the total egg mass that can be produced by a female of a given size. Then, rather than simply describing the relationship between egg number, egg size, and female size from data or as a geometric constraint of body size, we may believe that it is adaptive to have egg number and egg size change in response to maternal and environmental conditions. Thus, we would develop an optimality model. Model components may be derived from a regression model or from mechanistic considerations. Obviously the less "biology" there is in the model the greater the likelihood of producing erroneous predictions. When the value of a life history characteristic depends on characteristics of other individuals in the population (see "Life history patterns: correlations within Atlantic salmon"), we can use game theory models which allow us to consider frequency dependence in optimal life history strategies.

The criterion for validating an optimality model is that it predicts the observed field values when fitness is maximized. If the model fails in this regard it is assumed that a trade-off has been incorrectly specified or omitted. Mechanistic models may be able to predict the general form of a relationship, but they may not be able to specify parameter values. The principle of fitness maximization permits the estimation of parameter combinations. Hence it is possible to generate a set of possible suites of parameter values. Working with such combinations it is then possible to predict the outcome of changes in parameter values due to environmental change, for example. Two types of predictions are possible: first, those arising under the assumption that relationships (e.g., the amount of energy devoted to growth versus reproduction) remain constant, and second, those arising under the assumption that relationships change. The second type of prediction may be a consequence of phenotypic plasticity or of genetic change. In the former case the response will be immediate and the underlying assumption is that selection has molded the norm of reaction to maximize fitness. In the latter case the optimality model can predict only the final outcome, not the trajectory between the initial and final combinations. In this case short-term predictions likely will be most reliably made using the assumption of fixed relationships. To make a prediction of the trajectory between the two states, we must add another component, the genetic control of the traits.

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Genetic models

Optimality models predict equilibrium conditions but not the trajectory that led to them. As a consequence, novel perturbations which would not have molded a reaction norm cannot be dealt with by optimality models. A genetic model contains all the components of a mechanistic model plus the assumption that parameters are genetically variable. For a single trait X, the relevant equation is

$$R_X = h_X^2 S_X$$

where R_X is the response to selection (the change in the trait value X), h_X^2 is the heritability of trait X, and S_X is the selection differential (the difference between the population value and the parental value). For two traits, X and Y, we must also consider the correlated response of trait Y to selection on trait X, the genetic correlation between the two traits, the heritabilities of each trait, and the two phenotypic variances associated with each trait. Also, if selection acts on both traits, the equations become more complex but no additional genetic parameters are required. The important message is that a genetic model requires considerably more information than the previous modeling approaches. Each pair of traits requires the estimation of 6 (co)variances. If the changes in the environment are within the range normally experienced by the fish or we wish to predict equilibrium trait combinations, as in a geographic comparison, the optimality approach is preferred because it requires fewer data. On the other hand, if we wish to predict trajectories of changes in life history resulting from changes outside the normal range, then a genetic model is necessary.

Approach to comprehensive understanding: empirical studies

Long-term monitoring

Long-term monitoring programmes provide one means of obtaining data relevant to the construction of a general life history model of Atlantic salmon. Most importantly, long-term data provide estimates of the temporal variability associated with life history traits. Data collected concurrently on several life history traits would also permit direct and indirect estimates of the parameters required of a general life history model. In addition, one could use long-term baseline data to identify those traits most sensitive to unanticipated environmental or demographic change.

To minimize financial costs, long-term monitoring of life history traits could represent relatively small-scale projects that are constituent parts of existing research or stock assessment programmes. For example, temporal variation in the frequency of parr maturity, a parameter thought to increase with juvenile growth and adult fishing mortality, with consequences for population biomass (Myers 1984), could be obtained from random samples of parr taken over a period of a few days every autumn. These data could then be analyzed with reference to other life history data collected concurrently from the same population. Efforts should be made to maximize the information obtained from such monitoring programmes, including the archiving of samples (e.g., scales, adipose tissue) for future analysis.

Table 1. Number of Atlantic salmon populations for which life history data have been measured for a minimum of 10 years.

Life history data	Number of populations
Life history character	
Parr length	0
Incidence of parr maturity	1
Smolt length	2
Smolt age	7
Smolt-to-grilse survival	6
Seawinter:multiple seawinter salmon ratio	16
Grilse sex ratio	3
Grilse length	5
Fecundity	1
Egg size	0
Life history trait combination	
Smolt-to-grilse survival – fecundity	0
Smolt-to-grilse survival – smolt age	2
Smolt-to-grilse survival – smolt length	1
Smolt-to-grilse survival – grilse length	2
Smolt-to-grilse survival – incidence of parr maturity	0
Smolt-to-grilse survival – sex ratio	1

Note: Data collated from Appendix 2 in Hutchings 1998.

A minimum of 10 years of data is required to obtain reliable estimates of the variance associated with life history traits. There are at least 24 populations throughout the range of Atlantic salmon for which 10 or more years of data exist for at least 1 life history trait (see Appendix 2 of Hutchings (1998) for more details). Ranked by frequency of occurrence, life history characters for which long-term data are most readily available include grilse:multi-sea-winter salmon ratios, smolt age, smolt-to-grilse survival, and grilse length (Table 1). However, despite the apparently large number of populations for which long-term data have been collected, there are exceedingly few populations for which characters relevant to life history analyses have been measured concurrently for 10 or more years. Indeed, long-term data on a metric of survival and at least one additional life history character are available for only two populations, Western Arm Brook and Conne River (both in Newfoundland; Table 1). There are no populations for which long-term data are available on both survival and fecundity, or on both survival and incidence of parr maturity.

The near absence of long-term data on relevant life history traits from the same population makes it extremely difficult to construct and test general life history models for Atlantic salmon. But, despite this deficiency of data, long-term monitoring programmes should not be entered into without careful consideration of the variables that warrant measurement and those that do not. In addition, when collecting long-term data, one must be aware that many rivers may contain more than one genetic stock of salmon (Saunders 1981). Thus, variation in measured traits may reflect temporal variation, variation among stocks, or temporal changes in relative abundance of different stocks. Data collection programmes must be sufficiently rigorous to allow

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for discrimination among these different sources of variation.

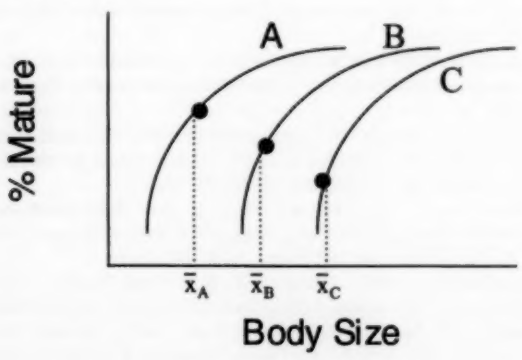
Manipulative experiments

Much of the information for variation in life history strategies in salmonids comes from comparisons between populations (e.g., in the mean age at smolting, mean percentage maturing at different ages, etc.). Although such data can be instructive in revealing the phenotypic plasticity that can occur in life history traits, they are also misleading if used to predict how a single population might respond to environmental changes. This is a consequence of the fact that each population has its own composition of genotypes and hence its own average reaction norm (Stearns 1992). For example, the shape of the relationship between body size at a given age and probability of maturing may differ among populations (as a result of population differences in growth or mortality rates). If mean values for both body size and percent mature are obtained from these different populations, it is possible to obtain a negative relationship between size and likelihood of maturity across populations, even though the relationship is positive within each of them (Fig. 2). The among-population trends thus tell us nothing about the underlying causal mechanisms (e.g., the relative genetic and phenotypic contributions). Such information can be revealed only by manipulative experiments designed to test the life history responses of fish of different origin to a range of environmental conditions.

The simplest such experiments are so-called "common garden" trials, in which fish from two or more populations are reared in a common environment (e.g., Nicieza et al. 1994). If there is no difference in response between fish of different origin, this suggests that the reaction norms for the different populations are very similar and any geographical variation in the measured life history traits is of environmental rather than genetic origin. However, experiments that do reveal population differences in response to a common environment are more difficult to interpret, especially since many common garden trials are carried out in an environment (e.g., a hatchery) that is markedly different from that experienced by any of the source populations. A more satisfactory (but logistically more difficult) experimental design is to carry out reciprocal transplants, which monitor the response of two or more populations when reared in each other's natural environment. The reciprocal nature of the rearing environments means that information on reaction norms is obtained independently for each population and population differences in phenotypic plasticity are immediately apparent.

An alternative approach is to carry out phenotypic manipulations, where phenotypic variation is generated by appropriate manipulations of the environment. While the nature of some of the relationships shown in Fig. 1 has been tested by such manipulation experiments (e.g., the link between growth rate and smolt age (Thorpe et al. 1989)), these have inevitably mostly been carried out in the laboratory or hatchery. A challenge for the future is therefore to carry out phenotypic manipulation experiments in conditions that more clearly resemble the natural environment.

Fig. 2. Hypothetical relationships between the size of salmon at a given age in three different populations (A, B, and C) and their likelihood of becoming sexually mature that year. The solid lines show the reaction norm within each population, while the dots indicate the mean values for each of the populations that might have been obtained during a short-term study. An among-population comparison using these mean values would indicate a negative relationship, while the true causal relationship is always positive.



Summary

Due to their economic importance and wide geographic range, Atlantic salmon are particularly well studied. Because of this, we have been able to construct a diagram illustrating the correlations among individual life history traits. But despite this level of understanding, we still lack an understanding comprehensive and quantitative enough to allow us to predict how the entire life history should respond to environmental changes or to changes in specific parts of the life history. Thus, we propose several general courses of action designed to enhance our ability to predict how the life history of Atlantic salmon should respond to change. First, we must continue to collect data, especially long time series in individual systems. Next, we must synthesize the available information, using models to tie together complex patterns and relationships. Finally, we must design experiments that will allow us to assess phenotypic plasticity and how specific phenotypes arise from different environmental influences and separate this from genetic influences and constraints.

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Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids

Ian A. Fleming

Abstract: The breeding system of Atlantic salmon (*Salmo salar*) is shaped both by natural selection for offspring production and by sexual selection for access to mating opportunities. These evolutionary forces operate with differing intensities in the two sexes to shape their breeding behaviour and tactics. Female breeding success is largely dependent on egg production, access to breeding territories, and nest quality and survival. By contrast, male breeding success is largely determined by access to ovipositing females. As such, the breeding system of Atlantic salmon is similar to that of other members of the subfamily Salmoninae. However, early male maturity, a common pattern within the Salmoninae, reaches its greatest expression in both terms of frequency and magnitude of the mature male size difference in Atlantic salmon. Despite generalities, spawning populations of Atlantic salmon are not static, as they exhibit spatial and temporal variability in demography (e.g., spawner density, sex ratio, age at maturity, and body size). Events, both natural and anthropogenic (e.g., exploitation, habitat alteration, and climatic changes), affect this variability and ultimately shape the breeding system.

Résumé : La reproduction chez le saumon atlantique (*Salmo salar*) est déterminée tant par la sélection naturelle, liée à la production d'une descendance, que par la sélection sexuelle, liée aux occasions d'accouplement. Ces forces évolutionnaires agissent avec des intensités différentes chez les deux sexes pour modeler leur comportement et leurs stratégies de reproduction. Le succès de la reproduction chez la femelle est largement dépendant de la production des oeufs, de l'accès aux territoires de reproduction, de la qualité du nid et de la survie des larves. Par contre, le succès de reproduction des mâles est lui largement déterminé par l'accès aux femelles pondeuses. Il se trouve que le système de reproduction du saumon atlantique est similaire à celui d'autres membres de la sous-famille des salmoninés. Cependant, la maturation précoce des mâles, phénomène commun chez les salmoninés, trouve son expression la plus forte, tant en termes de fréquence que d'importance de la différence de la taille des mâles matures, chez le saumon atlantique. Malgré certaines caractéristiques constantes, les populations reproductrices de saumon atlantique ne sont pas statiques : leurs caractéristiques démographiques montrent une variabilité spatiale et temporelle (p. ex., densité des reproducteurs, rapport des sexes, âge à la maturité et taille). Divers événements naturels et anthropiques (p. ex., exploitation, altération de l'habitat et changements climatiques) influent sur cette variabilité et, ultimement, façonne la biologie de la reproduction de l'espèce.

[Traduit par la Rédaction]

Introduction

Breeding systems are the description of the relation between parental investment in offspring production and mating behaviour, incorporating the study of gamete production, parental care, potential rates of reproduction, mating resources, mate acquisition, number of mates, and mate choice (Reynolds 1996). They are the outcome of competition among individuals to maximise their reproductive success within constraints imposed by the opposite sex, environment, and phylogeny. Breeding systems are therefore tightly linked to life history and are shaped by events occurring on both temporal and spatial scales. The purpose of this paper is to: (1) review the breeding system of Atlantic salmon, comparing it to that of other species within the subfamily Salmoninae (the genera *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus*) and (2) assess the implications of spatial and temporal variability in demography, particularly in relation to human disturbance, for the breeding system of Atlantic salmon.

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I.A. Fleming. Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway. e-mail: ian.fleming@ninatrd.ninaniku.no

The breeding system of Atlantic salmon

Reproductive investment and maturity

The breeding system of Atlantic salmon is a reflection of high investment in each reproductive bout, coupled with differences between the sexes in the allocation of the investment. In anadromous populations, both males and females expend about 59% of their total energy reserves to breed (Table 1), with larger individuals expending more than smaller individuals (Jonsson et al. 1991*a*, 1997). Moreover, only 11% of the spawners, on average, survive to breed another year (Table 1), though in some populations it may be as high as 43% (Ducharme 1969).

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Table 1. Reproductive characteristics of Atlantic salmon relative to other members of the subfamily Salmoninae. Data are means and ranges (in parentheses) of population means derived from some key references in the literature (see Appendix 1).

Species	% Energy loss at reproduction	% Repeat breeding	Gonadosomatic index (%)		Egg size (mg)[1]	Body size variation	Max. difference in ♂ length ((max – min)/min)	% Early ♂ maturity	♀ Nest defence
			Female	Male					
Salmo salar (Atlantic salmon)									
Anadromous	59 (52 – 65)	11.0 (0.7–42.5)	22.2 (20.1–25.7)	4.1 (2.3–5.8)	105 (94–127)	♂ > ♀	8.91 (5.00–13.30)	53[p] (2–100)	Nesting
				8.0[p] (4.7–10)					
Resident	—	30	17.3 (17.2–17.4)	—	87 (72–116)	♂ > ♀	1.17 (0.67–1.67)	—	Nesting
S. trutta (brown trout)									
Anadromous	—	34 (5–69)	18.5 (15.0–25.4)	2.9 (2.7–3.0)	85 (70–101)	♂ > ♀	3.27 (0.83–7.70)	22 (0.6–62)	Nesting
Resident	47 (46–48)	64.6	12.9 (9.9–15.8)	2.3 (1.9–2.6)	59 (48–76)	♂ > ♀	1.89 (1.23–4.55)	—	Nesting
Oncorhynchus nerka (sockeye salmon)									
Anadromous	73 (71–75)	0	17.8	3.0 (2.1–3.4)	105 (69–132)	♂ > ♀	1.16 (0.66–1.41)	5[j] (0–12)	Nesting and after
				4.3[j]					
Resident		0	12 (11.4–12.8)	2.7 (2.6–2.8)	85 (81–89)	♂ > ♀	0.61 (0.38–0.83)	—	Nesting and after
O. kisutch (coho salmon)	—	0	20.7 (19.4–24.0)	5.8 (5.2–6.4)	188 (91–297)	♂ > ♀	1.88 (1.12–2.44)	19[j] (0.4–46)	Nesting and after
				6.8[j]					
O. keta (chum salmon)	79	0	17.4	3.7 (3.2–4.1)	239 (164–282)	♂ > ♀	0.30 (0.17–0.45)	2[j] (0–6.9)	Nesting and after
O. tshawytscha (chinook salmon)	85	0*	19.0 (17.8–21.1)	6.1 (5.4–6.7)	251 (138–378)	♂ > ♀	2.26 (1.23–6.13)	<<1[p] (0–12)	Nesting and after
				9.0[p]				8[j] (0–36)	
O. gorbuscha (pink salmon)	72	0	16.8 (16.1–17.4)	5.2 (4.9–5.4)	162 (136–197)	♂ > ♀	0.38 (0.24–0.55)	0	Nesting and after
O. masou (masu salmon)									
Anadromous	—	0*	27	4	144 (124–162)	♂ > ♀	5.18 (4.35–5.73)	Parr and jacks	Nesting and after

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Table 1. (*Concluded*).

Species	% Energy loss at reproduction	% Repeat breeding	Gonadosomatic index (%)		Egg size (mg)[1]	Body size variation	Max. difference in ♂ length ((max – min)/min)	% Early ♂ maturity	♀ Nest defence
			Female	Male					
O. mykiss (rainbow trout)									
Anadromous	—	10.0 (0.6–31.3)	14.9 (14.5[2]–15.3)	—	101 (95–106)	♂ > ♀	3.48 (1.46–5.50)	Yes	Nesting
Resident	—	26 (18–33[3]	14.6 (8.3–22.6)	5	65 (51–77)	♂ > ♀	1.45 (1.15–1.85)	—	Nesting
O. clarki (cutthroat trout)									
Anadromous	—	20 (5–36)	—	—	101	♂ > ♀	3.02 (2.42–3.38)	Yes	Nesting
Resident	—	35 (25–44)	11.6	—	63	♂ > ♀	1.24 (1.12–1.36)	—	Nesting
Salvelinus malma (Dolly Varden char)									
Anadromous	—	26 (5–52)	17.1 (16.4–18.0)	4.4	73 (60–85)	♂ > ♀	1.87 (0.70–3.70)	Yes	Nesting
Resident	—	35 (34–36)	10.5	8.9	28	♂ > ♀	0.53	—	Nesting
S. fontinalis (brook char)									
Anadromous	—	21	13.9[2]	—	45	♂ > ♀	2.71 (1.96–3.46)	Yes	Nesting
Resident	—	24 (12–32)	13.2 (10.0–16.8)	1.5	46 (34–55)	♂ > ♀	1.34 (0.62–2.80)	Yes	Nesting
S. alpinus (Arctic char)									
Anadromous	52	41 (32–50)	16.4 (12.8–18.6)	4.4	56 (20–76)	♂ > ♀	2.33 (0.72–3.95)	Yes	Nesting
				6.7[p]					
Resident	—	61 (33–84)	18.4 (11.9–24.3)	2.8	47 (33–64)	♂ > ♀	1.95 (0.14–4.40)	—	Nesting and rarely after
S. namaycush (lake trout)	—	53 (6–79)	14.6 (12.3–17.6)	3.1	75 (44–122)	♂ > ♀	0.97 (0.64–1.77)	No	None, no nest
Hucho hucho (huchen)	—	64 (51–77)	15.5	3	79 (57–100)	♂ > ♀	1.78 (1.03–2.52)	—	Nesting

[1]Converted to fresh egg weight using relationships of Fleming and Ng (1987) and Jonsson et al. (1996) where necessary.
[2]Gonad weight calculated from individual egg weight and fecundity data.
p = mature male parr.
j = early maturing "jack" males that have spent a short duration at sea.
*Mature male parr may survive to breed again.

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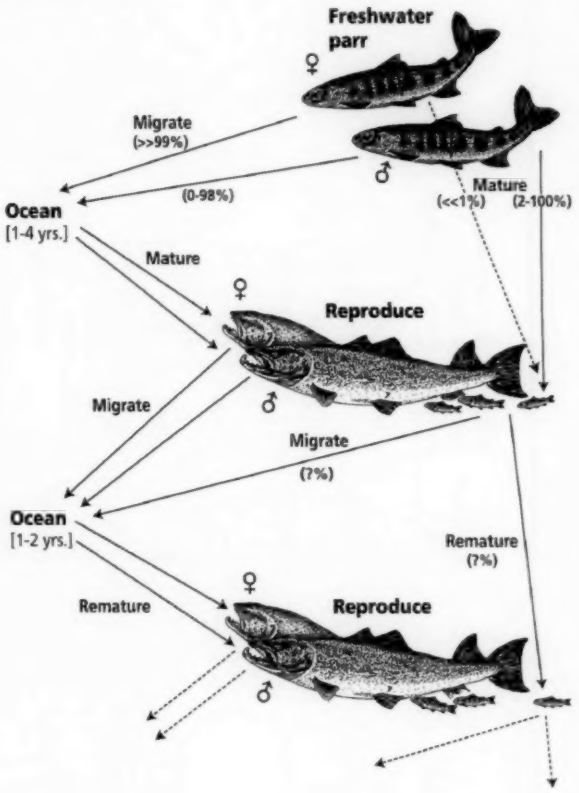
Such high reproductive investment appears to be surpassed only by that of the semelparous Pacific salmon (Table 1), that have no possibility of repeat breeding (except early maturing male parr of some masu (Tsiger et al. 1994) and chinook salmon populations (Unwin et al. 1999)). Among the iteroparous Salmoninae, including Atlantic salmon, paired contrasts of anadromous and resident forms of species, to control for phylogeny (Harvey and Pagel 1991), show that anadromy in general is associated with a significantly reduced probability of repeat breeding (t_7 = 3.77, P = 0.007; arcsine transformed data from Table 1). The apparent increase in reproductive investment that accompanies anadromy reflects the additional costs of longer migrations, which are traded off against benefits such as increased body size. The exception to this is the resident form of sockeye salmon, "kokanee," that appear phylogenetically constrained to being semelparous like their anadromous conspecifics. Interestingly, the degree of iteroparity of anadromous and resident forms is correlated (r = 0.926, n = 8 species, P = 0.009), suggesting species-specific effects of breeding systems.

In Atlantic salmon, the probability of repeat breeding decreases with increasing fish size, reflecting a general increase in energy expended during reproduction (Jonsson et al. 1997). In addition, males are less likely to survive the breeding season than are females (reviewed in Fleming 1996), which may explain why they are less likely to repeat breed (Anonymous 1968; Shearer 1992; but see MacDonald 1970). This occurs despite similar energy expenditures by the sexes during reproduction, suggesting that costs, other than energy, of the intense male–male competition for mating opportunities (e.g., wounding and risk of predation; Jonsson et al. 1990; Fleming et al. 1997) are partly responsible. The greater propensity for repeat breeding by females than males is a pattern common to other iteroparous Salmoninae (e.g., *Salmo trutta* (Evans 1994), *Oncorhynchus mykiss* (Busby et al. 1996), *Savelinus malma* (Armstrong and Morrow 1980) and *S. fontinalis* (Hutchings 1993)).

Female Atlantic salmon can mature after as little as a year in the ocean or as long as 4 yr (Fig. 1). Rarely, do females mature in freshwater without having first migrated to the ocean to feed (e.g., Power 1969; Hutchings 1986; Hindar and Nordland 1989; Verspoor and Cole 1989; Prouzet 1990). It is likely that they cannot achieve a body size in fresh water where the benefits of early maturity (pre-reproductive survival) outweigh the costs (e.g., reduced fecundity and competitive ability) (see also Hutchings and Jones 1998). At maturity, anadromous females invest approximately 22% of their body weight in gametes, which is comparable to that of other anadromous Salmoninae, but greater than that of non-anadromous forms (t_{19} = 3.68, P = 0.002; Table 1). There is a tendency for anadromy to be associated with greater female gamete investment as a percentage of body weight (paired contrasts, t = 2.45, n = 7 species, P = 0.050; arcsine transformed data from Table 1). The reduced probability of repeat breeding associated with anadromy theoretically favours an increase in present versus future reproduction (cf. Williams 1966; Stearns 1976; Roff 1992; Jonsson and Jonsson 1993; Hutchings and Jones 1998).

In energetic terms, the ovaries of female Atlantic salmon constitute 28–29% of their total energy reserves at spawning

Fig. 1. Life history tactics associated with reproduction observed within anadromous populations of Atlantic salmon. Arrows indicate major life history transitions (i.e., mature versus migrate) by male and female salmon, with the range among populations in the percentage of individuals of each sex following the different courses (derived from the literature) in parentheses.



time (Jonsson et al. 1991*a*, 1997). This represents about half of the energy expended during maturation, upstream migration and reproduction combined. Egg production is thus a major investment for females, shaping their reproductive behaviour. Interestingly, gamete investment by both female and male Atlantic salmon is similar to that of the semelparous Pacific salmon despite their differences in reproductive investment (i.e., energy loss). This suggests that the latter invests more heavily in activity such as breeding competition and nest guarding (Table 1), and in the development of traits for competition, such as secondary sexual characters.

In terms of allocation of the investment in egg production, Atlantic salmon and other iteroparous Salmoninae tend to produce smaller eggs than the semelparous Pacific salmon (comparing anadromous forms: t_{11} = 4.26, P = 0.001, Table 1; see also Rounsefell 1957). There may be a greater selective premium for egg size in the semelparous species, for example due to higher juvenile densities and competition at emergence, however, phylogenetic effects due to shared evolutionary histories cannot be ruled out. Egg size also tends to be larger among anadromous than resident forms of species,

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an effect that is independent of phylogeny (paired contrasts: $t_7 = 4.35$, $P = 0.003$). This, however, may partly result from allometric constraints, as egg size typically increases with female body size within (e.g., Balon 1980; Groot and Margolis 1991; Fleming 1996) and across the Salmoninae species ($r = 0.734$, $n = 15$, $P = 0.002$, Table 1 and length at maturity data from Hutchings and Morris 1985; see also Rounsefell 1957). Nevertheless, the range of egg sizes among anadromous and resident populations often overlap, despite differences in female body size. This indicates allometric constraints, if they exist, are not great and that selection has likely been important, though the selective forces (e.g., juvenile competition, habitat, quality of female care, predation) are poorly understood.

In Atlantic salmon and many other members of the Salmoninae, males show a greater recognisable diversity of life history tactics associated with reproduction than females. As a result, the variability in body size within populations tends to be greater among mature males than females (Table 1). This is partly a consequence of male fecundity being less constrained by body size than that of females. Male gonadal investment, measured as gonadosomatic index, is about a fifth that of females across the Salmoninae (mean ± SD = 21.5 ± 6.1%; Table 1). For anadromous Atlantic salmon males, this investment averages 4% of their body weight and in energetic terms, this is less than a sixth of that of females (excluding production costs; Jonsson et al. 1991*a*, 1997). Furthermore, unlike females, male gonadal investment as a percentage of their body weight does not appear to be influenced by anadromy within the Salmoninae (paired contrasts: $t = 0.367$, $n = 4$ species, $P = 0.738$; arcsine transformed data from Table 1).

The greater variability in male than female body size at maturity also reflects the use of alternative tactics by males to gain access to fertilisation opportunities, such as sneaking, where small size becomes advantageous. As a result, early male maturity is a common phenomenon among the Salmoninae, particularly the anadromous forms (Table 1). This propensity for early male maturity together with larger maximum sizes attainable, on average, through anadromy may explain the greater range in body size of male spawners within anadromous than resident populations of Salmoninae (part contrasts: Wilcoxon signed rank test, $Z = 2.52$, $n = 8$ species, $P = 0.012$). The only Salmoninae species reported not to have early male maturity are the lake trout that do not deposit eggs in nests and the pink salmon where all fish almost invariably mature at the early age of 2 yr.

Early male maturity reaches its greatest expression in terms of frequency and magnitude of the mature male size difference in Atlantic salmon (Table 1). In some populations, up to 100% of males have been estimated to mature early as parr during their life history. They do so before ever having migrated to sea and at a body weight that is often two orders of magnitude smaller than that of the anadromous males with whom they compete for spawnings. Thus two distinct male phenotypes frequently coexist on the spawning grounds: large, anadromous males that fight for access to females and small, early-maturing parr males that sneak access to females (Fig. 1, Table 1).

The two male phenotypes of Atlantic salmon likely coexist as a result of the combined effects of both frequency- and status-dependent selection (*sensu* Gross 1996). Frequency-dependent selection occurs when the relative success gained by using one tactic (i.e., fight versus sneak) is influenced by the tactics used by other members of the population. For example, anadromous males may be more successful, on average, than mature parr when anadromous males are rare, but less successful when they are common. Thus, no single tactic is evolutionarily stable, but rather a mixture of the two tactics evolves. When the relative success gained by using a tactic depends on the individual's competitive ability or "state" relative to others in the population, status-dependent selection may operate as well. For example, only the largest or most dominant males may be able to effectively adopt the parr tactic while other males are better off delaying maturity, because the costs of early maturity will outweigh the benefits for them.

The discovery of a heritable basis to male parr maturity (Nævdal et al. 1976; Glebe and Saunders 1986), together with evidence of a strong environmental effect associated with individual growth rate (e.g., Alm 1959; Saunders et al. 1982; Berglund 1992), provide support for evolution by frequency- and status-dependent selection. It appears that a genetically determined threshold related to growth rate or a state (e.g., lipid, weight) exists, which once achieved results in early male maturity (Thorpe 1986; Bohlin et al. 1990; Rowe et al. 1991). Frequency-dependent selection, as affected by the intensity of mate competition, environmentally induced differences in growth rates among males, and age-specific mortality rates, likely determine this polygenic threshold (Bohlin et al. 1990; Hutchings and Myers 1994). Similar mechanisms probably explain the existence of early male maturity in other salmonid species.

Breeding behaviour

Female breeding behaviour in Atlantic salmon, like that in other Salmoninae species, appears to be shaped, to a large extent, by natural selection for offspring survival. For instance, the timing of reproduction in Atlantic salmon has likely evolved in response to selection for favourable conditions for spawning, embryo incubation, and juvenile emergence and subsequent feeding. While egg developmental rates are highly temperature dependent (Hamor and Garside 1976; Peterson et al. 1977), they tend to vary little among Atlantic salmon populations (Wallace and Heggberget 1988), though some local adaptation exists (Brännäs 1988). By comparison, considerable variability exists in the timing of reproduction, which can differ by as much as 4 months among populations (reviewed in Fleming 1996). The timing of reproduction may thus be the principal mechanism by which larval emergence is adjusted to meet local environmental conditions (e.g., temperature) both among (Heggberget 1988, Jensen et al. 1991) and within rivers (Summers 1996; Webb and McLay 1996). This pattern is also common to Pacific salmon (Brannon 1987; Healey 1991; but see Tallman 1986; Hendry et al. 1998) and likely to the other Salmoninae species.

Intraspecific competition may be another factor affecting the timing of reproduction. Early-breeding females may have ready access to the highest-quality spawning sites, but may be susceptible to nest destruction from the digging activity of later-breeding females. This is an effect best known

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from the semelparous Pacific salmon that spawn at high densities (e.g., Schroder 1982; van den Berghe and Gross 1989; McPhee and Quinn 1998), but is also now being recognised among several iteroparous species of Salmoninae (e.g., Kitano 1996; Blanchfield and Ridgway 1997), including Atlantic salmon (Fleming 1996). Although early-emerging offspring may incur heavy predation initially, they may subsequently outcompete late-emerging conspecifics and incur reduced predation because of their greater size resulting from early growth (Metcalfe and Thorpe 1992; Brännäs 1995). A trade-off thus exists between early and late breeding, and this trade-off is likely affected by female phenotype. For example, female body size, through its positive affects on nest depth, may reduce susceptibility to nest destruction. Female egg size can affect offspring size at emergence and thus growth, social status, susceptibility to starvation, and predation (reviewed in Fleming 1996).

The female decision as to where to spawn appears to be affected by several factors, including habitat conditions, local adaptation, traditionality, and intrasexual competition. Female breeding territories tend to be concentrated in areas having suitable habitat requirements for spawning and egg incubation. In Atlantic salmon, such areas often occur on the upstream side of riffles or gravel bars, where the concentration of fines is low (10–15% by weight) and permeability (>900 $cm \cdot h^{-1}$), and thus dissolved oxygen levels, are high (e.g., Peterson 1978; Crisp and Carling 1989; Gustafson-Greenwood and Moring 1991; reviewed in Fleming 1996). There is also circumstantial evidence of local homing by females to specific locations within rivers where they had resided as juveniles (Saunders 1967; Heggberget et al. 1988; Youngson et al. 1994). Such local homing may be an adaptation (i.e., heritable) to match genotypes with environments. Alternatively, this behaviour may be a form of traditionality, which evolves when complete resource assessment is costly, and previous experience (e.g., as a juvenile) provides insight into current resource quality (cf. Warner 1988, 1990). Local homing may lead to population substructuring among Atlantic salmon within river systems (e.g., Verspoor et al. 1991; King et al. 1993; Tessier et al. 1997). Active choice of breeding locality, however, may be constrained to some extent by overt aggression from other nesting females (Jones 1959; Webb and Hawkins 1989; Fleming et al. 1997) and environmental conditions (e.g., water flow).

Like other members of the Salmoninae with the exception of lake trout, Atlantic salmon females construct nests within the gravel substrate of their breeding territories. This serves to protect their developing embryos principally from predation, but also from gravel shifts caused by freshets and digging by other females, desiccation during low water, and freezing. To do so, females use a series of tail-beating sequences; a female turns on its side, pressing its caudal fin against the gravel, and then rapidly lifts the caudal fin, creating a water vortex that displaces gravel (detailed in Jones and Ball 1954; Jones 1959). During excavation of the nest, such digging bouts are concentrated within the developing nest pit and may be interspersed with periods of probing, where the female crouches in the nest pit with her anal fin erect, apparently assessing nest readiness. This process, from nest initiation to egg deposition, may take from 1 h to 2 d (Webb and Hawkins 1989). Nest covering begins immediately after egg deposition, as the female attempts to rapidly protect her eggs. At this stage, digging bouts are more frequent and spatially less concentrated than before, occurring around the upstream edges of the nest, with the displaced gravel lifted onto the nest thus covering the eggs. Nest covering slowly switches to excavation as a new nest pit begins to emerge in front of the previous one and the process is repeated.

The number of nests a female Atlantic salmon constructs varies directly with their body size, with small one-sea-winter females (ca. 1 kg) producing 3–5 nests and large, multi-sea-winter females (6–7 kg) producing as many as 14 nests (Fleming et al. 1996, 1997). Successive oviposition events are usually less than a day apart, though the time between such events may range from 4 h to 9 d (Fleming 1996). The nests may be constructed within one or more redds (i.e., the contiguous area of disturbed gravel containing a female's nests) (Webb and Hawkins 1989; Baglinière et al. 1990; Barlaup et al. 1994), the degree to which is likely affected by factors such as female size, degree of spawning habitat discontinuity and female competition. Like the number of nests constructed, the number of eggs a female deposits in each nest varies directly with her size and inversely with the number of previous ovipositions she has made (Fleming 1996). Females usually complete nesting within 5–6 d during which time they aggressively defend their nesting territories. Once nesting is completed, females appear not to defend their nests, descending from the spawning grounds to a nearby pool. This is a pattern common to the iteroparous Salmoninae and contrasts with that of the semelparous species that defend their nests from reuse until death (Table 1). Nest defence is energetically expensive and risky (e.g., exposure to injury and predation) and the benefits may not offset the costs for iteroparous species that often breed at lower densities and have the opportunity to survive to breed another year.

Male Atlantic salmon, like those of all Salmoninae, do not participate in nest acquisition or construction and their breeding behaviour is principally shaped by sexual selection for access to mating opportunities. Male–male competition for mates is intense because the operational sex ratio (i.e., the number of sexually active males to females) is commonly male-biased, and often highly so, a pattern commonly seen in the Salmoninae (e.g., Schroder 1982; Fleming and Gross 1994; Quinn et al. 1996; Blanchfield and Ridgway 1997). Female Atlantic salmon are typically active on the spawning grounds for 5–6 d, while males can remain reproductively active for a month or more (Webb and Hawkins 1989; Fleming et al. 1996, 1997). This coupled with asynchronous female spawning and the male ability to spawn rapidly and repeatedly generates the intense male competition for access to spawning females. Hence, sexual selection is likely responsible, in large part, for the evolution of the secondary sexual characters developed by anadromous males (e.g., hooked lower jaw or "kype" and red breeding colouration; reviewed by Fleming 1996) (cf. Fleming and Gross 1994; Quinn and Foote 1994) and of the alternative reproductive tactic of male parr maturity. Moreover, it may explain the apparently large energetic investment by anadro-

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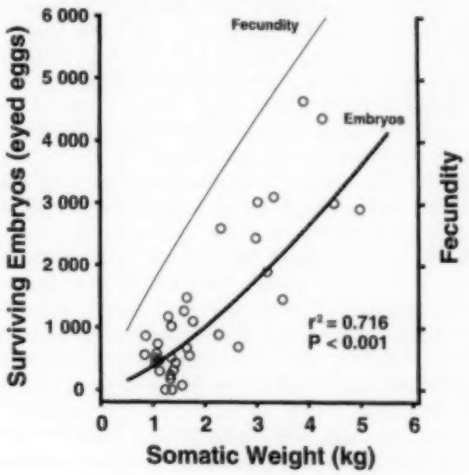
mous males in behavioural activity on the spawning grounds (Jonsson et al. 1991*a*, 1997) and their considerably higher levels of aggression than females (Fleming et al. 1997).

The intense aggression among males commonly results in the formation of local dominance hierarchies in the vicinity of nesting females and one or more anadromous males may occupy secondary or "satellite" positions slightly downstream of the female and dominant male (Belding 1934; Jones 1959; Järvi 1990; Fleming et al. 1996, 1997). Relative body size appears to be one of the principal determinants of dominance (Järvi 1990; Fleming et al. 1996). This may explain the observation that small anadromous males wander more within rivers than larger males (Belding 1934; Webb and Hawkins 1989; Baglinière et al. 1991), apparently attempting to find access to breeding females. Similar dominance hierarchies may also form among the mature male parr in attendance (Jones and King 1952; Myers and Hutchings 1987). Courting of the female, however, remains principally the realm of the dominant male (described in detail in Jones 1959; Fleming 1996). Nesting females do express mate choice, directing over half of all their aggression towards males (Fleming et al. 1997). Moreover, they may depart from their nest sites when repeated intrusions and aggression among males occur, not returning until male dominance relations stabilise. Females may gain genetic benefits (i.e., quality genes) from such mate choice, as well as safety from disruption and injury during spawning, reduced risk of infection and predation, and fertilisation assurance. Intense male–male competition, however, likely puts some constraints on the freedom of female choice.

Most spawnings involve a single anadromous male, one or more mature male parr, and the female. Matings involving two or more anadromous males do, however, occur and their frequency appears to increase with male bias in the operational sex ratio and (or) the density of anadromous males (Fleming et al. 1997). During spawnings with multiple anadromous males, the first two males usually position themselves on either side of the female, with subsequent males darting along their outsides or attempting to squeeze underneath (Mjølnerød et al. 1998). Mature male parr, present at the spawning, attempt to squeeze deep into the nest next to the female's vent. Shortly after spawning, the anadromous males usually depart, as do many of the mature male parr, though both may return later to partake in one or more of the female's subsequent spawnings.

Fig. 2. Relation between female body size (somatic weight) and breeding success (surviving embryos) for wild Atlantic salmon from the River Imsa, Norway (thick solid line; $y = 0.027 \times (\text{somatic weight})^{1.385}$). Data are from a series of experiments in semi-natural stream environments (Fleming et al. 1996, 1997), where the number of surviving offspring (i.e., eyed eggs) was determined directly by excavation of nests. For comparison, the relation between female body size and fecundity for wild Atlantic salmon from the River Imsa is shown (thin solid line; $r^2 = 0.81$, $P < 0.001$; Jonsson et al. 1996).



Female breeding success

Female breeding success (i.e., number of embryos surviving till just prior to hatching) in Atlantic salmon shows a strong, positive relation to body size principally as a consequence of increased fecundity (Fig. 2). Fecundity alone, however, cannot fully explain the relation because female egg number typically increases at a declining rate with body size (see also Randall 1989; Fleming 1996; Hutchings and Jones 1998), while breeding success increases exponentially. Thus large females are producing fewer eggs but are achieving higher breeding success per unit body size than are small females.

Body size is important for both fecundity and the ability to spawn eggs and have them survive incubation. Spawning areas within rivers may appear non-limiting, however, females show preferences for particular sites, often clumping their nests in such areas (e.g., Heggberget et al. 1988; Sættem 1995). Under such circumstances, female body size because of its association with competitive ability (Fleming et al. 1997) can be important in attaining and defending preferred nesting localities. Moreover, reduced access to nesting sites may result in delays in spawning that cause declines in egg viability (e.g., Brännäs et al. 1985) or even retention of eggs unspawned (Beall and Marty 1983), though the latter is rare (Baglinière et al. 1990; Jonsson et al. 1990; Fleming et al. 1997). Female body size can also influence nest quality through its effects on nest construction. For example, larger females construct deeper nests than smaller females (White 1942; Jones 1959; Crisp and Carling 1989; Fleming et al. 1997), potentially reducing the susceptibility of their nests to destruction resulting from gravel shifts, river desiccation, freezing, and nest superimposition by later-breeding females. Large females also produce larger eggs than do small females (reviewed in Fleming 1996), which may be related to the superior parental care (i.e., nest quality) that they can provide (Sargent et al. 1987; van den Berghe and Gross 1989). These larger eggs often give rise to larger juveniles (Glebe et al. 1979; Kazakov 1981*a*; Thorpe et al. 1984) that are competitively advantaged and have higher survival (e.g., Bagenal 1969; Wankowski and Thorpe 1979; reviewed in Fleming 1996).

These findings suggest that attempts to predict female reproductive contribution based solely on female fecundity (e.g., Elson 1975; Chadwick 1985; Mangel 1996) will be in-

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complete. As van den Berghe and Gross (1989) point out, such an approach overlooks important aspects of body size for female success, under-representing the contributions of large females and over-representing those of small females.

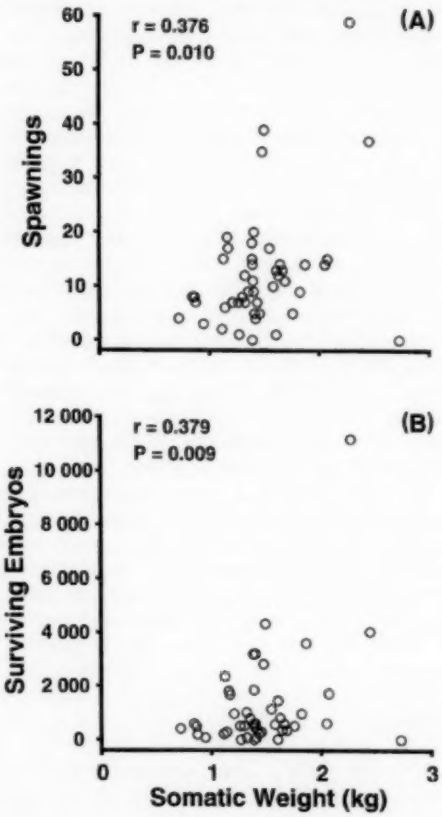
Given the importance of female body size for breeding success in Atlantic salmon and the existence of adequate genetic variation (Gunnes and Gjedrem 1978; Rye and Refstie 1995; Jónasson et al. 1997), why have female not evolved to be larger? Such evolution is almost certainly opposed by selection during other life-history episodes. For example, foraging to obtain a larger body size involves risks, particularly in terms of survival (Abrahams and Dill 1989; Holtby and Healey 1990). Delaying maturity an extra year in the ocean to attain greater size may cost a 50–93% probability of mortality (Table 4.3.4.2, Anonymous 1996). Large body size may also make ascent and breeding difficult and risky during low water flows in rivers (Jonsson et al. 1991*b*). Further, the associated advantages of large egg size for early juvenile life may be compromised due to increased mortality during incubation resulting from poor intergravel oxygen conditions (van den Berghe and Gross 1989; Quinn et al. 1995). There may also be negative genetic covariances with other traits caused by antagonistic pleiotropy that constrain further evolution (Endler 1986), though this is poorly understood within salmon. In addition, selection pressures fluctuate through time, affecting the course of evolution (e.g., Kalisz 1986; Madsen and Shine 1993), as factors such as breeding density, growth rate, and river discharge vary. Thus, while large body size is favoured during breeding, its evolution must reflect comprises with alternative selection pressures, environmental heterogeneity, and genetic constraints.

Male breeding success

The breeding success of male Atlantic salmon is principally a function of four things: (1) access to females; (2) female egg deposition; (3) fertilisation competition; and (4) embryo survivorship and development (e.g., female nest quality). For anadromous males, access to mating opportunities increases with body size (Fig. 3A) and because the majority of spawnings involve single anadromous males (Fleming et al. 1996, 1997; see also Webb and Hawkins 1989), it tends to be highly correlated with breeding success ($r = 0.904$, $P < 0.001$). Large body size facilitates male dominance, increasing not only access to spawnings but also the ability to monopolise them (Fleming et al. 1996, 1997). The explanatory power of male body size in terms of mating and breeding success (Fig. 3), however, is only moderate, suggesting that males have alternative routes by which to gain access to matings. For example, some anadromous males adopt female breeding colouration (i.e., a dark lateral band along the length of the body) and remain quiescent, resting on the bottom next to the female (Fleming et al. 1997). This behaviour appears to attract little aggression from the dominant male and may allow the subordinate to remain near the female during oviposition.

Like anadromous males, large body size facilitates dominance among mature male parr (Jones and King 1952; Myers and Hutchings 1987), with the smallest individuals apparently becoming excluded from mating opportunities (Thomaz et al. 1997). Improved access to matings facilitated by larger size, however, will be at the cost of decreased

Fig. 3. Correlations between male body size (somatic weight) and mating (A) and breeding success (B) for wild Atlantic salmon from the River Imsa, Norway. Data are from a series of experiments in semi-natural stream environments (Fleming et al. 1996, 1997; Mjølnerød et al. 1998). Mating success was measured as the number of spawnings a male participated in and breeding success as the number of surviving embryos (i.e., eyed eggs) a male fathered. The latter was determined directly for 61% of spawnings and estimated for 39% based on male rank order of nest entry at spawning or rank dominance in the spawning aggregation (see Fleming et al. 1996, 1997).



crypsis. A trade-off thus exists, which is likely affected by the intensity of parr competition, and availability and size of refuges from which to sneak access to spawning females.

Males may be choosie with regards to female size (cf. Sargent et al. 1986; Foote 1988) and nesting stage (i.e., number of times a female has previously spawned), both of which affect the number of eggs she deposits at a spawning (Fleming 1996). Females may, in turn, adjust the number of eggs they deposit for given males as a form of mate choice, as has been observed in other fish (van den Berghe et al. 1989), though never investigated in salmonids.

Male fertilisation success at a spawning event depends largely on the number of competitors, with sperm competition ensuing when more than one male breeds simultaneously with the female. Under such circumstances, male proximity to the female's vent at spawning and sperm precedence become important for fertilisation success in Atlantic

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salmon (Mjølnerød et al. 1998), as in other Salmoninae species (Schroder 1982; Chebanov et al. 1984; Maekawa and Onozato 1986; but see Foote et al. 1997). Among anadromous males, large body size facilitates proximity through its effects on dominance and thus increases sperm precedence (Fleming et al. 1997, Mjølnerød et al. 1998). Moreover, larger males are likely to release more spermatozoa because of their larger ejaculate volumes (Kazakov 1981*b*; Gjerde 1984), providing them with an additional advantage (Mjølnerød et al. 1998). Small males, however, may be able, on occasion, to use their size to advantage to rapidly sneak next to the female's vent at spawning, as has been observed in sockeye salmon (Foote et al. 1997). Male fertilisation success also appears to be negatively affected by high levels of spawning activity (Mjølnerød et al. 1998), likely because of a decline in ejaculate volume, and spermatozoa concentration and activity (Kazakov 1981*b*; Gjerde 1984).

Despite their small size, mature male parr can attain significant fertilisation success. Within populations, secondary male fertilisation, a large part of which is likely due to mature parr, has been estimated to range from 11 to 40% of all eggs (Jordan and Youngson 1992; Thomaz 1995). At individual spawning events, parr success has been observed to range from 0–89%, with an individual male parr fathering up to 34% of the eggs (Morán et al. 1996; Thomaz et al. 1997). Much of the success of mature male parr comes from their small size, which allows them to remain within the female's nest and close to her vent, thus providing sperm precedence at egg deposition. Their small size, however, constrains gamete production, as mature male parr have gonad weights only 6% that of anadromous males (unpublished data from the River Imsa, Norway). To some extent, mature male parr compensate for this by investing relatively more of their resources into gonad production. They have gonadosomatic indices about twice that of anadromous males (Table 1), as well as higher spermatozoa concentrations and motility and longer spermatozoa life span (Daye and Glebe 1984; Gage et al. 1995). Even so, mature male parr appear to be sperm limited (Thomaz et al. 1997).

Parr breeding success, like that of anadromous males, is affected by the number of like competitors (i.e., other mature male parr). Individual success has been shown to be density dependent, declining with increasing numbers of parr (Hutchings and Myers 1988; Thomaz et al. 1997). Such density dependence is in agreement with the hypothesised frequency-dependent maintenance of the alternative male tactics, but does not provide definitive evidence of its existence. The evolution and maintenance of the alternative male tactics in Atlantic salmon, as in other Salmoninae, is one of the most poorly studied aspects of the breeding system.

Effects of spatial and temporal variability in demography

Heterogeneity and human disturbance

The breeding system of Atlantic salmon is influenced by a range of events, both natural and anthropogenic, that occur across spatial (e.g., freshwater and oceanic habitats) and temporal (i.e., within and across generations) scales that affect life history and reproduction. Environmental heterogeneity (e.g., in resource abundance, temperature, water flow, and predation) in both time and space affects the demography of salmon populations during spawning and, hence, the breeding system. One of the most obvious outcomes of this is the variability generated in the annual number of spawners within a population (coefficients of variation within populations: median 50.6%, range 18.0–112.8%, $n = 19$ populations with 7 or more years of data; Appendix 2). More subtle outcomes may be mediated through, for example, changes in growth rate due to annual heterogeneity in resource abundance and (or) temperature that subsequently influence age- and size-at-maturity (Hutchings and Jones 1998; Metcalfe 1998). As a result, populations will fluctuate in both the mean and the variability in body size of spawners (Fig. 4). Similarly, the sex ratio of spawners will vary (Fig. 5), because the sexes often experience different temporal environments due to differing ages of maturity, both as parr and anadromous adults. Such demographic variability affects the breeding system, altering the intensity of competition and the distribution of breeding phenotypes, and ultimately, the genetic structure of subsequent generations. The breeding system of Atlantic salmon has likely evolved in response to such temporal and spatial variability in selection and is probably robust to environmental heterogeneity, at least within its natural range. Human disturbance, through exploitation of spawning populations, however, may compound the natural demographic variability and shift populations into regions where the variability may threaten sustainability (cf. Hutchings 1996).

In such situations, releases of hatchery-reared Atlantic salmon are often used to supplement and (or) restore populations. This practice, however, almost invariably impacts the breeding system of the natural population. For instance, releases of cultured fish as parr, which have experienced rapid growth due to hatchery conditions, may result in an increase in number of males reaching the growth rate/state threshold for parr maturity (cf. Gross 1991). This will thus alter the intensity of parr–parr breeding competition. Rapid juvenile growth can also decrease age-at-smolting (Metcalfe et al. 1989; Økland et al. 1993; Hutchings and Jones 1998; Metcalfe 1998) and subsequently, sea-age-at-maturity, a pattern that has been observed in hatchery-supplemented populations of Atlantic salmon (e.g., Christensen and Larsson 1979; Sharov and Zubchenko 1993; Petersson et al. 1996). Moreover, the difference in sea-age-at-maturity between the sexes is likely to decline, shifting the sex ratio of anadromous spawners towards females (Fig. 6). While this shift may be affected by an increase in the proportion of males maturing as parr (i.e., decreased male freshwater survival), it appears to be more a function of changes in relative sea-ages and thus marine survival of the sexes. The sex ratio of anadromous salmon shows little relation to the proportion of males maturing as parr ($r = 0.162$, $P = 0.655$, $n = 10$ populations; Appendix 2), though such among population comparisons may hide within-population responses (Marschall et al. 1998). All of the above changes will affect the form of breeding competition as the frequency of the different breeding phenotypes change, altering selection and impacting the breeding system.

Finally, interbreeding between cultured and wild populations may have a number of genetic consequences, including the introduction of traits altered by domestication, out-

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Fig. 4. Annual variation in the mean and coefficient of variation (CV) of body weight for male (open symbols) and female (closed symbols) anadromous Atlantic salmon returning to the rivers Umeälven, Sweden, and Imsa, Norway. Data are from McKinnell et al. (1994) and the fish trap records of the Ims Research Station, Norwegian Institute of Nature Research.

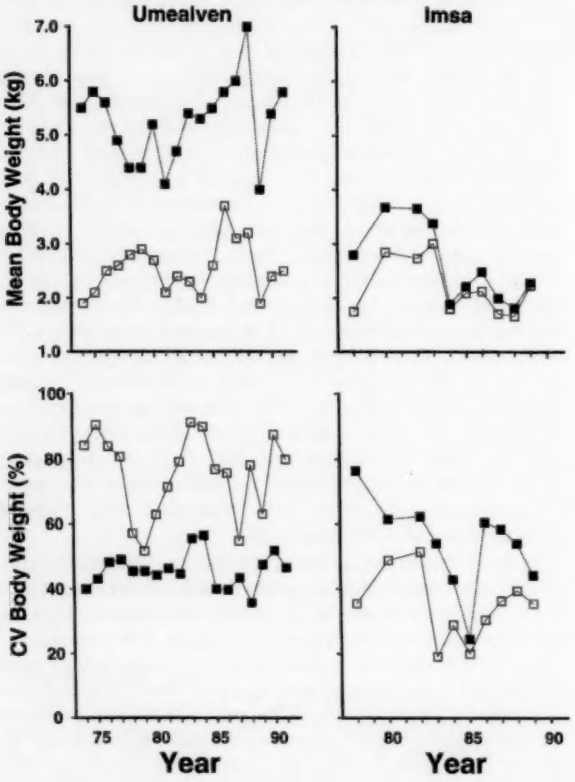
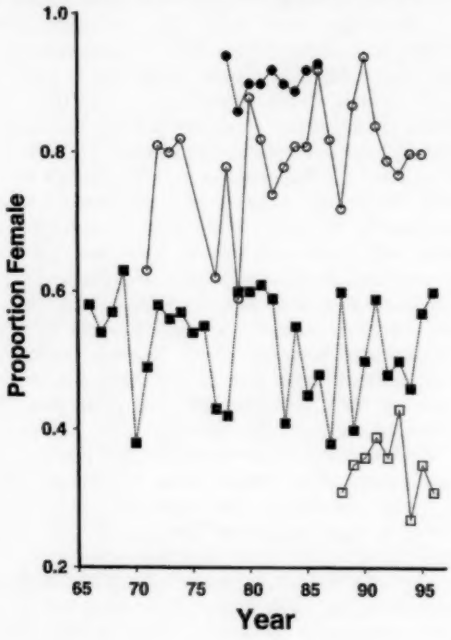


Fig. 5. Annual variation in the sex ratio of anadromous Atlantic salmon returning to the Northeast River (●) and Western Arm Brook (○), Newfoundland, and the Girnock (■) and Baddoch Burns (□), Scotland. Data are from O'Connell et al. (1996) and fish trap records kindly provided by Alan Youngson and David Hay, Scottish Office of Agriculture, Environment and Fisheries Department, Freshwater Fisheries Laboratory, Pitlochry.



breeding depression and changes in between- and within-population genetic variances (reviewed in Hindar et al. 1991; Waples 1991; Fleming 1995; Ryman et al. 1995). However, the degree of these effects will be mediated by the reproductive capability of introduced cultured Atlantic salmon, which appears to be impeded relative to that of wild fish (Jonsson et al. 1990; Fleming et al. 1996, 1997).

The distribution of alternative life history phenotypes on the spawning grounds may also vary in response to anthropogenic impacts that: (*i*) reduce overall population size; (*ii*) alter environmental conditions; and (*iii*) decrease survivorship of particular segments of the population. Reductions in overall population size will affect density-dependent processes, including juvenile growth and survival (reviewed in Gibson 1993) and breeding competition (Fleming et al. 1997). These, in turn, are likely to affect the distribution of different life history tactics, such as male parr maturity and sea-age-at-maturity (e.g., Myers et al. 1986; Randall et al. 1986; Hutchings and Jones 1998), which ultimately affect the dynamics of the breeding system. Similar responses are likely to be associated with human-induced changes in environmental conditions (e.g., micro- and macro-climate changes, eutrophication and river regulation) that affect growing conditions and spawning habitat.

Selective mortality of particular segments of Atlantic salmon populations, for example due to size-selective fisheries (Allen et al. 1972; Bielak and Power 1986; Dempson et al. 1986), will also alter the distribution of phenotypes on the spawning grounds. First, there could be a shift in the mean size/age of spawners. This would alter selection on age-at-maturity (e.g., Stokes et al. 1993), including the propensity for males to mature as parr (Caswell et al. 1984; cf. Gross 1991). Second, size-selective fisheries can alter the variance in the size of competitors on the spawning grounds. Directional and stabilizing selection (harvesting the largest and (or) smallest fish) will decrease variance and disruptive selection (harvesting intermediate size fish) will increase variance. This will, in turn, affect the intensity of breeding competition, particularly among anadromous males. Third, size-selective fisheries in many populations are likely to target females more than males because of their older sea-ages at maturity (Fig. 6). The resultant bias in the sex ratio will negatively affect the effective population size (reviewed in Lande and Barrowclough 1987) and increase the intensity of male–male competition (i.e., more males competing for each female). This latter effect will be strongest among the mature male parr, which are not exposed to fishing mortality.

The response of Atlantic salmon to human-induced impacts on their breeding system will, at least initially, involve

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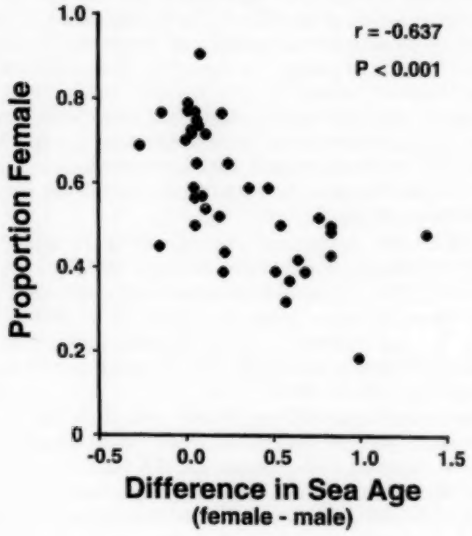
Fig. 6. Correlation between the difference in mean sea-age-at-maturity of female and male Atlantic salmon and the sex ratio of anadromous spawners (proportion female). Data are from 38 populations from the North Atlantic and Baltic (see Appendix 2). Proportion female was arcsine transformed prior to analysis.



environmentally mediated changes (i.e., phenotypic plasticity) in behaviour and life history strategies, and may over time result in genotypic changes as well. The speed and ability of the breeding system to respond (through plasticity and genetic change) will be important in determining the extent to which salmon populations become compromised by anthropogenic effects. Effective management and conservation of Atlantic salmon will thus depend on predictive knowledge about such responses, an area that is poorly understood. The importance of this is compounded by the close link between the breeding system and the life history of salmon.

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Oncorhynchus kisutch

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Fleming, I.A. (unpublished data: male gonadosomatic index, Chilliwack River, B.C.: hooknose males, mean = 5.2%, n = 11, range 4.1–6.3%; jack males, mean = 6.8%, n = 7, range 5.8–8.0%; Capilano River, B.C.: hooknose males, mean = 6.4%, n = 7, range 5.3–7.8%)

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Salvelinus fontinalis

(Carlander 1969; Blanchfield and Ridgway 1997; Hutchings 1993; Jonsson and Jonsson 1993; Lee 1971)

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Hucho hucho

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Appendix 2

The Atlantic salmon populations from differing regions used to examine variability of spawning population size ([1]), the correlation between sex ratio and the difference in mean sea-age-at-maturity of females and males ([2]), and the correlation between sex ratio and proportion of mature 1+ male parr ([3]). Published and unpublished data sources are given by region: citations in parentheses have been referenced elsewhere in the manuscript.

Baltic

Ume,[1] Kalix,[2] Lule,[2] Ångerman,[2] Indal,[2] Ljusne,[2] Dal,[2] and Mörrum[2]

(McKinnell et al. 1994)

Alm, C. 1934. Salmon in the Baltic precincts. Cons. Perm. Int. Explor. Mer, Rapp. P.-V. Vol. XCII.

Canada

Campbellton,[2] Terra Nova,[1,2] Middle Brook,[1,2] Biscay Bay,[1,2] Northeast,[1,2] Lomond,[1,2,3] Torrent,[1,2] Western Arm Brook,[1,2,3] Gander,[1,2] Conne,[1,2] Margaree,[2,3] Miramichi,[2,3] Restigouche,[2,3] St John,[2] Nepisiguit,[2] St Mary's,[2] LaHave,[2] Pigou,[2] Bouleau[2]

(Myers et al. 1986; Randall 1989; O'Connell et al. 1996)

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France

Elorn[2,3] and Adour[2,3]

(Prouzet 1990)

Scotland and Ireland

Girnock Burn,[1,2,3] Baddoch,[1] North Esk,[1] Burrishoole,[1] Shannon,[1] and Erne[1]

(Jordan and Youngson 1992; Shearer 1992; Alan Youngson and David Hay, personal communication)

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Norway

Imsa,[1,2,3] Måls,[2] Namsen,[2] Alta,[2] Orkla,[2] Eira,[2] Bævra,[3] Aurlandsvassdrag,[1] and Lærdal[1]

(Sættem 1995)

Bohlin, T., Dellefors, C., and Faremo, U. 1986. Early sexual maturation of male sea trout and salmon — an evolutionary model and some practical implications. Rep. Inst. Freshwater Res. Drottningholm, **63**: 17–25.

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Russia

Varzuga[2] and Kola[2]

(Jensen et al. 1997)

Spain

Narcea[2]

Prévost, E., Vauclin, V., Balglinère, Brana-Vigil, F., and Nicieza, A.G. 1991. Use of a technique to determine the sex of Atlantic salmon (*Salmo salar* L.) in the rivers of Asturias (Spain). Bull. Fr. Pêche Piscic. **323**: 149–159. (In French with an English abstract.)

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Movement, migration, and smolting of Atlantic salmon (*Salmo salar*)

Stephen D. McCormick, Lars P. Hansen, Thomas P. Quinn, and Richard L. Saunders

Abstract: A variety of movements characterize the behavioral plasticity of Atlantic salmon (*Salmo salar*) in fresh water, including movements of fry from redds, establishment of feeding territories, spawning movements of sexually mature male parr, movement to and from winter habitat, and smolt migration in spring. Smolting is an adaptive specialization for downstream migration, seawater entry, and marine residence. While still in fresh water, smolts become silvery and streamlined, lose their positive rheotaxis and territoriality, and begin schooling. Physiological changes include increased salinity tolerance, olfactory sensitivity, metabolic rate, scope for growth, and altered hemoglobin and visual pigments. Through their impact on the neuroendocrine system, photoperiod and temperature regulate physiological changes, whereas temperature and water flow may initiate migration. Smolt survival is affected by a limited period of readiness (a physiological "smolt window") and the timing of seawater entry with environmental conditions such as temperature, food, and predators (an ecological "smolt window"). Smolt development is adversely affected by acidity, pollutants, and improper rearing conditions, and is often more sensitive than other life stages. Unfortunately, the migration corridor of smolts (mainstems of rivers and estuaries) are the most heavily impacted by pollution, dams, and other anthropogenic activities that may be directly lethal or increase mortality by delaying or inhibiting smolt migration.

Résumé: Une grande variété de déplacements caractérise la plasticité comportementale du saumon de l'Atlantique en eau douce, notamment le départ des alevins qui quittent le nid, l'établissement de territoires d'alimentation, les déplacements génésiques des tacons mâles sexuellement matures, les allers-retours vers les zones d'hivernage, et la dévalaison des smolts au printemps. La smoltification est une spécialisation adaptative enn vue de la dévalaison, de l'entrée dans l'eau salée, et du séjour océanique. Alors qu'ils sont encore en eau douce, les smolts prennent leur livrée argentée et leur forme devient plus hydrodynamique, ils perdent leur rhéotaxie positive et leur territorialité, et commencent à se rassembler en bancs. Ils subissent des changements d'ordre physiologique : tolérance accrue à la salinité, sensibilité olfactive, métabolisme, potentiel de croissance et modification de l'hémoglobine et des pigments visuels. Par leur impact sur le système neuroendocrinien, la photopériode et la température régulent les changements physiologiques, tandis que la température et le débit peuvent déclencher la migration. La survie des smolts est affectée par l'existence d'une période limitée de condition optimale (une « fenêtre physiologique ») et par la synchronisation de l'entrée en eau salée avec des conditions environnementales comme la température, la nourriture, et la présence de prédateurs (une « fenêtre écologique »). Le développement des smolts est négativement affecté par l'acidité, les polluants, et les mauvaises conditions de grossissement, et ce stade est souvent plus vulnérable que les autres. Malheureusement, le corridor de migration des smolts (cours principal des cours d'eau et estuaires) passe par les eaux les plus fortement touchées par la pollution, les barrages, et d'autres activités humaines qui peuvent avoir un effet létal direct ou accroître la mortalité en retardant ou en empêchant la migration des jeunes saumons.

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S.D. McCormick.[1] Conte Anadromous Fish Research Center, Biological Resources Division, USGS, P.O. Box 796, Turners Falls, MA 01376, U.S.A.
L.P. Hansen. Norwegian Institute for Nature Research, Oslo, Norway.
T.P. Quinn. School of Fisheries, University of Washington, Seattle, WA 09195, U.S.A.
R.L. Saunders. St. Andrews Biological Station, Department of Fisheries and Oceans, St. Andrews, NB E0G 2X0, Canada.

[1]Author to whom all correspondence should be addressed.
e-mail: mccormick@umext.umass.edu

Introduction

Migration is the hallmark of salmon life history. When juvenile Atlantic salmon (*Salmo salar*) reach a certain size-related developmental stage in fresh water, they leave their rearing tributaries in spring and begin a journey that will take them downriver, through estuaries, and hundreds or thousands of kilometres to ocean feeding areas. Prior to and during this downstream movement, they display many complex physiological, behavioral, and morphological adaptations for seaward migration and life at sea. Along with these complex changes, smolts face other challenges: new food sources, diseases, parasites, and predators, which make the smolt stage a critical one in which mortality can be high and variable. Growth opportunities for salmonids are generally better at sea than in fresh water, but natural mortality may be

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higher in the marine environment. The "decision" as to whether the population or individual gains greater advantage from migration or residence depends on the balance of these two factors (see Jonsson and Jonsson 1993; Thorpe 1994). The much greater fecundity of anadromous females and reduced mortality of eggs and fry in fresh water are the apparent rewards for undertaking the risks of anadromy (Gross 1987).

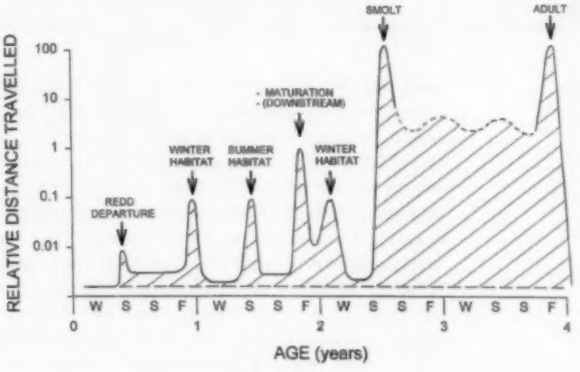
In addition to the smolt migration, Atlantic salmon make other movements in fresh water that are important to their survival (Fig. 1 and next section), including movements to winter habitat and spawning movements of mature parr. Because smolting, winter survival, and sexual maturation require high levels of stored energy, feeding and growth are of prime importance during freshwater residence. Movements, then, are mainly associated with attaining the maximum amount of food or a suitable habitat while avoiding predation or other sources of mortality.

The downstream movement of smolts is a "true" migration, being highly directed, temporally synchronous, and occurring in virtually all individuals of the appropriate developmental stage. It is less clear whether the movements made by Atlantic salmon before smolting are migrations and no single definition of this term is accepted by all or even most biologists. Dingle (1996) defined migratory behavior as "persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence." He also considered that migration is persistent, straightened-out (directed), undistracted by resources that would ordinarily halt it, has distinct departing and arriving behavior, and requires a special allocation of energy. Under these terms, salmon movements in fresh water would not be considered migrations unless they were directed (e.g., upstream or downstream) and could not be stopped by encountering a particular resource (e.g., habitat or food). We do not know whether all Atlantic salmon movements fulfill this definition, but in many cases they clearly do not. While it is beyond the scope of the present undertaking to classify salmon movements, we will conservatively interpret most (but not all) nonsmolt movements in fresh water as meeting the more general criteria of "movement" rather than the more restrictive "migration." Although some of these considerations are semantic, they facilitate our understanding of the external stimuli and internal motivation that underlie the initiation and cessation of juvenile salmon movements.

We also note that salmon can successfully complete their life cycle without migrating. Maturation of male as parr is common in many Atlantic salmon populations and there are also several populations of "dwarf" Atlantic salmon in Newfoundland in which both females and males mature in streams (Sutterlin and Maclean 1984). There are also many "land-locked" populations in which smolts migrate downstream but reside in lakes rather than the sea (Berg 1985). This capacity to complete their life cycle without anadromy further demonstrates the plasticity of salmon life history traits.

This paper reviews the movements and migrations of juvenile Atlantic salmon in fresh water from "swim up" fry to the smolt stage and discusses possible motivations for these behaviors. We also describe the smolting process in terms of physiology, morphology, and behavior and discuss the possible role of olfactory imprinting in relation to these factors. Finally, some factors affecting the mortality of smolts during downstream migration and the transition from fresh to salt water are reviewed and fruitful areas of future research are presented.

Fig. 1. Movement patterns of Atlantic salmon. Filled area represents the range of estimated distances travelled for a given life history stage. A representative 4-year life cycle (2-year-old smolt) is shown on the x-axis (W = winter, S = spring and summer, F = fall). Relative values for distance travelled are approximate and taken from literature discussed in section on "Fry and parr movement." Smolt migration distance includes both river and initial ocean migration.



Fry and parr movement

We have divided the movements of juvenile Atlantic salmon prior to the smolt transformation into five phases: (1) movement of fry from the vicinity of their redds; (2) establishment and occupation of feeding territories; (3) spawning movements of sexually mature male parr; (4) shifting from summer feeding territories to winter habitat; and (5) descent from nursery streams to lower reaches of some rivers in late autumn as a forerunner or component of smolt migration.

Movement of fry from redds

Spawning areas are typically gravel beds with moderate current velocity and depth (Fleming 1996). When their yolk is largely or entirely absorbed, the fry emerge from the gravel, mainly at night (Gustafson-Marjanen and Dowse 1983; Crisp and Hurley 1991*b*). Crisp and Hurley (1991*a*) noted that fry disperal rates were low at water velocities similar to their preferred velocities (25–70 cm@s^{-1}) and that dispersal rates were higher at lower water velocities. There is, then, a tendency for the newly emerged fry to seek areas with moderate current velocity rather than calm water. R.L. Saunders (unpublished observations) noted that fry that had recently completed yolk absorption delayed first filling of their swimbladders in high water velocities. In their study of movements of underyearling fry in a small coastal stream during August–September, Saunders and Gee (1964)

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observed that most fry were found in shallow riffles with more moderate current velocity compared to the faster riffles and coarse substrate occupied by older, larger parr. In their first summer, fry tended to remain in the area of their initial capture; those recaptured in adjacent areas were near where they were first observed. In early December fry had moved into nearby parr habitat. However, the sensitivity of many studies of stream-dwelling fishes to movement outside the study area is low and there is good reason to question the assumption of limited movement (Gowan et al. 1994).

The apparent tendency of fry to remain in localized areas is important in several respects. First, juvenile salmonids are incubated with full-siblings and maternal half-siblings (same mother and different fathers) and the general tendency of salmonids to associate with siblings (reviewed by Brown and Brown 1996) suggests that families might remain together for some time after emergence. Such nonrandom distribution patterns could result in marked variation in family-specific growth and survival. Second, limited movement by juveniles, regardless of family, has important management implications. Hatchery-reared fry may not move far from release sites; hence, releases should be in small groups, widely dispersed in suitable shallow riffles (Crisp 1995; McMenemy 1995).

Movements of parr

Parr, in their second or succeeding juvenile years, are typically found in fast flowing riffles in association with rough gravel substrate and they defend feeding territories against other parr and heterospecifics. (Kalleberg 1958; Keenleyside and Yamamoto 1962; Gibson 1966, 1993). The size of the territory depends on the size and density of parr, food availability, the size and roughness of the substrate, and current velocity (Kalleberg 1958; Grant et al. 1998). Territorial and efficient position-holding behaviors (Arnold et al. 1991) enable parr to maximize their opportunity to capture floating aquatic and terrestrial invertebrates (Godin and Rangeley 1989; Gotceitas and Godin 1992). This positioning is facilitated by a reduced swimbladder volume and resulting increased density of parr at high-water velocity (Saunders 1965).

Atlantic salmon are not confined to stream riffles at the parr stage but may also be in slow-moving water such as pools (e.g., Saunders and Gee 1964). Parr tended to remain in the type of habitat where they were first observed but moved from riffles to pools during periods of low water, usually returning to riffles when water level rose again. Parr displaced up- or down-stream were subsequently observed at their original capture sites within 14–39 days (Saunders and Gee 1964). Saunders (1960) noted that where brook trout (*Salvelinus fontinalis*) were abundant in pools, their preferred habitat, salmon parr were absent from these pools whereas in allopatry salmon occupied pools.

In addition to movements within the natal stream, salmon may move to other rearing sites. For example, in a large Finnish river (the Teno), fry left the main river and entered tributaries too small for spawning, where they grew faster and attained a larger size as smolts than in the main (spawning) stream (Erkinaro and Niemelä 1995). Parr often move into the small tributaries during summer and remain there until they leave as smolts one or more years later. The small tributaries have much rougher substrate than the spawning stream, not only producing more food organisms but also better winter habitat. In some instances parr may move to cooler tributaries to avoid high temperatures (R.A. Cunjak, personal communication). Armstrong et al. (1997) observed that a few 1-year-old and older fish moved into an area that had been depleted of juvenile salmon but that most fish did not move far from their small territories. Thus, fish that colonize new areas may represent a small number of highly mobile individuals. It is unclear whether all fish have a weak tendency to move and movement is influenced primarily by environmental factors, or whether there are mobile and sedentary individuals in each population as reported for chinook salmon (*O. tshawytscha*; Bradford and Taylor 1997). We currently have a very limited understanding of the risks associated with parr movements and the rewards of colonizing new areas.

In many Newfoundland streams, parr move up or downstream to lakes within the stream system (Chadwick 1982; Hutchings 1986), where parr are observed singly or in small schools. Salmon parr from some streams may also spend weeks or months in estuaries during the summer (Cunjak et al. 1989, 1990; Power and Shooner 1966). Cunjak et al. (1989) reported that the larger parr in estuaries apparently went to sea as smolts whereas the smaller ones probably returned to their natal stream in autumn. Thus, although salmon parr generally have territories and a rather limited home range, they can occupy habitats ranging from riffles to pools and lakes within the stream system and even to estuaries. The extent to which population pressure influences the movement from riffles to other habitats is a subject needing further investigation.

Movements of mature male parr

Apart from the habitat choices of parr rearing in streams, some males become sexually mature and move up or down stream to spawning sites (Buck and Youngson 1982; Youngson et al. 1983). It was believed for some time that mature male parr were incapable of stimulating large anadromous females to spawn and that the male parr served only as satellite spawners, dashing in at the last second to contribute their milt (Jones and King 1952). During courtship, the large anadromous males repeatedly chase away the parr but cannot do so during the crucial moment when the large fish release their spawn. However, Hutchings and Meyers (1985) reported that sexually mature male parr are capable of spawning with anadromous salmon (grilse) in the absence of large anadromous males. Mature parr eat salmon eggs (Cunjak and Therrien 1996), which could have an important function in providing energy to replace that expended in the production of gonads and participation in spawning.

Movements to winter habitat

Juvenile Atlantic salmon take advantage of seasonally warm water to maximize food intake and growth but they must conserve energy during winter when food is less available and maintaining station in rapidly flowing water would have a high energy cost. Usually they enter spaces under or between stones, sometimes in excavations associated with redds made the previous autumn (Cunjak 1988; Erkinaro et al. 1994). The size of the "home stone" is usually correlated

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with the size of the parr (Cunjak 1988). Winter sites are often in the same area as summer feeding territories (Saunders and Gee 1964; Rimmer et al. 1983) but there is some movement, probably in response to changing physical and chemical conditions and the availability of food (Cunjak and Randall 1993; Cunjak 1996). Smirnov et al. (1976), Riddell and Leggett (1981), and Cunjak (1988) emphasized that parr have reduced daytime activity during winter, leaving their hiding places at night to feed. This is in keeping with the observation that salmon parr become negatively phototactic in winter (Rimmer 1980). Daytime hiding behavior in winter allows parr to maintain position without great expenditure of energy and may make them less vulnerable to predation at a time when they have a reduced escape response. Hiding in the stream bed does not entirely preclude salmon from feeding during winter. Riddell and Leggett (1981) and Cunjak (1988) observed that overwintering parr consume some food but the rates of consumption and digestion are probably quite low because low temperatures are only slightly above freezing in most salmon nursery streams during midwinter. Cunjak (1988) discussed the importance of winter feeding to maintain energy reserves in dealing with stresses associated with drastic physical and chemical conditions as well as those resulting from human activity.

Autumn downstream movement of presmolts

In some headwater tributaries the large parr, those likely to become smolts the following spring, depart their summer rearing areas and move downstream for some unknown distance, not necessarily entering an estuary or the sea (e.g., Meister 1962). R.L. Saunders (unpublished observations) marked large parr moving downstream past a counting weir on the headwaters of the Northwest Miramichi River, New Brunswick in the early 1960s. A few of these marked fish were recaptured the following spring at a counting weir farther down river, 12 km above head of tide. It was assumed that the marked fish spent the winter at some location between the two counting fences. Riddell and Leggett (1981) found large numbers of parr moving downstream and out of Rocky Brook (an upriver tributary of the Southwest Miramichi River) in autumn and that there was no smolt migration in Rocky Brook the following spring. Youngson et al. (1994) described a similar autumn migration of parr and their contribution to the fishery from Girnock Burn, an upriver tributary of the River Dee in Scotland. Such movement to larger, downriver habitats in winter may reflect a need for appropriate physical habitat or greater energy input than is available in the nursery stream. Riddell and Leggett (1981) suggested that the habitat which is suitable in summer and winter for smaller parr is unsuitable for larger parr because the gravel substrate is too small to provide refuge. In such salmon populations, one might view the smolt run as beginning with the downstream migration of large parr in late autumn. If salmon become imprinted to the odors of their nursery stream and this is the mechanism by which they return to that stream, imprinting in such stocks must take place no later than the autumn when they emigrate from their natal stream (Dittman and Quinn 1996).

Researchers and management agencies should consider these movements by juvenile salmon at various life stages. It is important to understand both the "typical" movement of juveniles and the full range of possible movements (Fig. 1). In addition, differences in behavior attributable to distinct populations or river habitats will be important to conservation of populations (Saunders 1981).

Smolt physiology

Extensive research on the physiology of smolting has been conducted over the last 20 years, due in part to the demands of the salmon culture industry and government enhancement programs that release billions of salmonid smolts annually. The extent of this research is exemplified by the five International Smolt Workshops that have been held since 1982, the proceedings of which have been published in the journal *Aquaculture* (Volumes 28, 45, 82, 121, and 168). Rather than comprehensively review this material (as has been done by McCormick and Saunders 1987, Hoar 1988, and Boeuf 1993), we will present an overview of smolt physiology that emphasizes factors that are relevant to our understanding of the population biology of Atlantic salmon and future research efforts.

Several morphological changes are obvious during smolting. The deposition of guanine and hypoxanthine in the skin and scales covers the parr marks and results in the external silvering that is characteristic of smolts. Reflective silvering is common to many pelagic fishes and is presumably adaptive for predator avoidance. Darkened fin margins also characterize Atlantic salmon smolts. Smolts grow more in length than weight, resulting in reduced condition factor (weight relative to length) (S.D. McCormick, unpublished results). Loss of total body lipid during smolting also reduces condition factor (Wedemeyer et al. 1980). It is unclear whether lower condition factor is part of an adaptive change in morphology during smolting (e.g., to increase swimming performance in open water) or if it results from the energetic demands of smolt transformation. The emergence of teeth and changes in body shape that have been found in coho salmon, *Oncorhynchus kisutch* (Gorbman et al. 1982) have not been demonstrated in Atlantic salmon.

Many of the physiological changes that occur in Atlantic salmon smolts in fresh water are adaptive for seawater entry. These include development of a high level of salinity tolerance, increased scope for growth in seawater, shift in visual pigments from porphyropsin to rhodopsin (the latter characteristic of ocean fishes, Alexander et al. 1994), change in hemoglobin to the adult isoforms (Koch 1982), and increased buoyancy (Saunders 1965). The development of salinity tolerance is obviously important to seaward migrants and has been the most widely studied physiological change that occurs during smolting. The mechanisms for increased hypoosmoregulatory ability include differentiation of the gill, gut, and kidney (McCormick and Saunders 1987). Increased gill Na^+, K^+-ATPase activity, number and size of gill chloride cells, and intestinal water permeability have been strongly linked to increased salinity tolerance during smolting (Boeuf 1993). Although parr can survive gradual acclimation to seawater (Duston 1994), smolts can directly enter seawater with minimal ionic disturbance (Hoar 1988). This heightened hypoosmoregulatory ability permits uninter-

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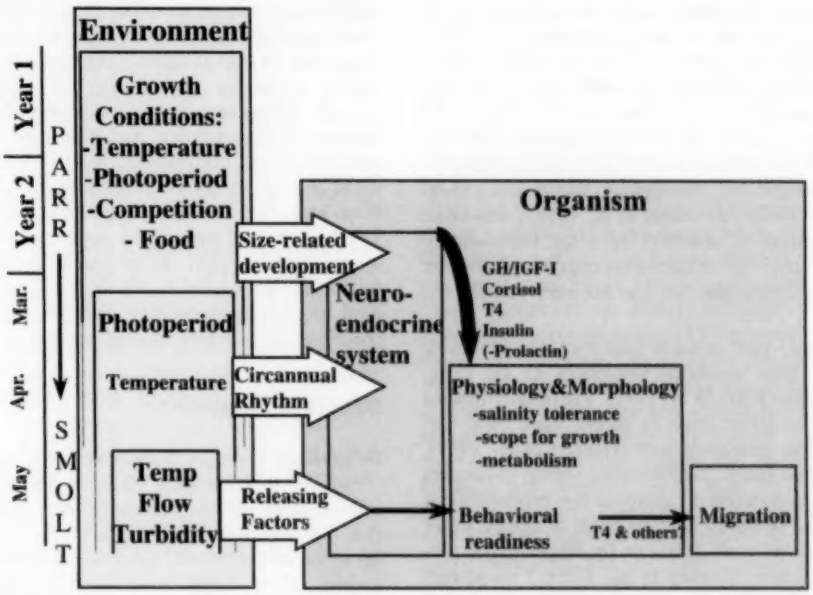
Fig. 2. Multiple interactions between the environment and the organism that lead to smolt development. Growth conditions such as temperature, food, photoperiod, and competition determine growth of Atlantic salmon parr. A critical size (or size-related development stage) is necessary for smolting to proceed and thus environmental conditions determine the age at which smolting occurs. Once this developmental stage has been reached photoperiod and to a lesser degree temperature regulate neuroendocrine changes that bring about physiological changes in spring. Releasing factors such as temperature, flow, and turbidity may have rapid effects (dashed arrows) to initiate downstream migration. Development of the smolt physiological condition (which presumably includes a behavioral readiness or a migration disposition), induced by prior development, photoperiod, and temperature, is necessary for releasing factors to initiate downstream migration (see also Baggerman 1960). The possible neuroendocrine or physiological mediators of these rapid effects are not currently known.



rupted feeding after seawater transfer, whereas nonsmolts experience high plasma ion concentrations and delayed feeding for several days (McCormick 1994). The increased salinity tolerance of smolts also permits decreased estuarine residence time (Tytler et al. 1978; McCormick et al. 1985) and improved swimming performance in seawater (Jarvi 1989), both of which may reduce exposure to estuarine predators. Smolts are adapted not just to survive in seawater, but to thrive there.

It should be emphasized that smolting is fundamentally a developmental phenomenon; juvenile Atlantic salmon must be of an appropriate size-related developmental stage or they will not smolt in response to environmental cues (Fig. 2). In the wild this translates to a lower age at smolting in southern latitudes with long growing seasons (1-year-old smolts in Spain, France, southern British Isles, and New England) and increasing smolt age with increasing latitude (usually 2–4 year old smolts; Wedemeyer et al. 1980; Hutchings 1998; Metcalfe 1998). The precise nature and proximate (neuroendocrine) regulators of this size-related development in smolting are unknown.

Of the environmental factors that regulate physiological development during smolting, photoperiod has the greatest influence. Seasonally advanced increases in daylength or out-of-phase photoperiod can advance smolting by many months (Duston and Saunders 1995). Although there is some evidence for an endogenous rhythm of smolting (Eriksson and Lundqvist 1982; Duston and Saunders 1990; McCormick et al. 1995*a*), increased daylength is probably necessary for complete smolting to occur. The capacity of photoperiod to affect smolting may be restricted at low temperatures (<3°C, McCormick et al. 1995*b*), indicating that temperature may be a controlling factor in smolting (Fry 1971). Temperature also has a role in the timing of smolt development that may be more direct and of particular importance in wild fish. Several laboratory studies indicate that increasing mean daily rearing temperatures from 2 to 10°C can advance smolting (as judged by peak gill Na^+, K^+-ATPase activity) by up to a month. In reviewing the influence of temperature on smolt development, McCormick et al. (1996) concluded that although increased temperature was not necessary for the completion of smolting, it acted with photoperiod to advance smolting and could act as a directive factor in the absence of photoperiod cues. High temperature increases the rate of loss of physiological smolt characteristics (Duston et al. 1991; McCormick et al. 1996) and has serious implications for smolt survival in the wild (discussed below).

The neuroendocrine system is the primary means of transmitting environmental change to physiological response and there is strong evidence that smolting involves the coordination of several endocrine systems (Bern 1978). This can be contrasted with metamorphic events in flounders and amphibians that are primarily stimulated by thyroid hormones,

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although other endocrine systems are certainly involved. Growth hormone, insulin-like growth factor I (IGF-I), cortisol, and thyroxine have all been implicated in the development of salinity tolerance in smolting and these hormones all increase during smolting (Hoar 1988). Increased daylength has a strong positive effect on growth hormone levels in smolts (Björnsson et al. 1989; McCormick et al. 1995*a*) and, to a lesser extent, stimulates plasma levels of IGF-I, cortisol, and thyroxine (McCormick et al. 1995*b*). Relatively little is known about the possible influence of temperature on these hormones during smolting of Atlantic salmon. Prolactin has a negative influence on salinity tolerance, perhaps through its antagonism of the action of growth hormone (Madsen and Bern 1992). Most of the evidence for the involvement of hormones in smolting has been in relation to their effects on salinity tolerance. Although thyroid hormones influence silvering, hemoglobin forms, and retinal pigmentation (Hoar 1988; Alexander et al. 1994), endocrine control of other aspects of smolting have not been widely examined. The influence of hormones on migratory behavior would be especially interesting but has not been widely examined in fishes.

Maturation of male parr reduces but does not eliminate the probability of later smolting (Saunders et al. 1982; Hansen et al. 1989; Berglund et al. 1991). Previously mature parr released into the River Imsa in spring were 30% less likely to migrate than immature parr (Hansen et al. 1989). Large mature parr can smolt the following spring (Saunders et al. 1994) and it is possible to increase the proportion of the mature males that smolt by keeping them in heated water during winter (Berglund et al. 1991) or by stripping the mature parr in the autumn (Hansen et al. 1989; Greenstreet 1992). Sex steroids have a negative effect on several aspects of smolt development including salinity tolerance and migratory behavior (Lundqvist et al. 1989; Berglund et al. 1994). However, sex steroids in previously mature salmon parr have returned to low levels well before completion of smolting in spring (Mayer et al. 1990; Shrimpton and McCormick, unpublished data) indicating that the negative influence of maturation on smolting may be part of developmental decisions determined well in advance of spring changes in smolt physiology (Metcalfe 1998). Although increased size results in greater incidence of mature male parr, maturation has a negative effect on growth in autumn (Berglund 1992). Maturation may therefore affect the probability of smolting simply by influencing fish size, causing some fish to fall below the size threshold for smolting. It remains to be seen whether other mechanisms are also invovled.

Although the patterns of smolt development vary among populations, the genetics of smolting have not received much research attention and there is conflicting information. Birt et al. (1991) found substantial differences between anadromous and nonanadromous populations of Atlantic salmon in Newfoundland. The anadromous stock had higher gill Na^+, K^+-ATPase activity, more and larger gill chloride cells, and greater silvering than a nonanadromous stock. Although no difference in salinity tolerance was found, the authors suggested this may have been due to the low salinity (32 ppt) used in these tests (other studies have used 35–40 ppt). Reduced salinity tolerance has been found in other nonanadromous stocks in Newfoundland (Burton and Idler 1984). In contrast, Staurnes et al. (1992) found no difference in gill Na^+, K^+-ATPase activity and silvering between anadromous and nonanadromous strains in Norway. Orciari and Leonard (1996) found that fish that originated from the Penobscot River, Maine, and from Icelandic rivers developed differently when transplanted in a tributary of the Connecticut River as fry; smolts from Icelandic stocks were smaller and migrated earlier than Penobscot or Connecticut river strains. These studies indicate that genetic factors are important in size at smolt development, intensity of physiological changes, and timing of migration. Population-specific differences in smolt development could be very important to conservation and restoration and deserve much more attention. For instance, the trajectory of smolt development and migratory behavior may be quite different in fish from long rivers (where physiological development may follow initiation of migration) compared to fish in short rivers where physiological development may precede migration. Extinction of stocks, as has occurred in southern New England, may make restoration difficult due to the loss of adaptive features characteristic of regions or watersheds.

Smolt migration

Behavioral changes during smolting

Numerous behavioral changes occur during downstream migration of smolts, including increased negative rheotaxis (i.e., downstream orientation) and schooling, decreased agonistic and territorial behavior, and increased salinity preference (Hoar 1988; Iwata 1995). Although endogenous rhythms in smolt-related behavior may occur, the studies described below strongly indicate that behavioral changes during smolting are dependent on environmental change. For instance, Gibson (1983) found that Atlantic salmon parr and smolts in artificial streams had similar agonistic behaviors that did not change in spring and concluded that smolt-related increases in buoyancy and seasonal increases in water velocity were necessary to cause decreased agression and downstream migration. Findings such as these also underscore the interelation between physiological and behavioral changes during smolting. Baggerman (1960) suggested that "migration occurs only when the animals are in the proper physiological condition (migration disposition) and at the same time under the influence of appropriate external stimuli which act as releasers." The interaction of internal developmental events, environmental "priming" factors (which bring about "migration disposition") and "releasing" factors is shown in Fig. 2. The importance of light, temperature, and water flow as releasing factors that act to initiate downstream migration of smolts is discussed below. It should be noted that most of these studies rely on correlations and there is little experimental evidence establishing the environmental factors that initiate migration. In addition to these environmental factors, other factors such as social cues (i.e., the presence of other migrants) may play a role in initiating downstream migration (Hansen and Jonsson 1985). The synchronous nature of smolt migration (occurring over a 3–6 week period in most populations) is due to the individual

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smolts reaction to these releasing factors and may have the adaptive value of overwhelming predators by sheer numbers.

Light

As discussed above, photoperiod is the seasonal "zeitgeber" that triggers a complex series of physiological events that prepare salmon for migration. Although photoperiod influences migratory behavior of Pacific salmon smolts (see Hoar 1976), there has been no direct investigation of the role of photoperiod in regulating behavioral changes in Atlantic salmon smolts. By analogy to other vertebrate migrations, photoperiod may act to increase activity (migratory restlessness or Zugunruhe) and make fish sensitive to other factors (releasing factors) that initiate migration. Thus, photoperiod may determine the range of dates during which migration may occur but other factors such as water temperature, flow, and turbidity may act as releasing factors.

Smolt migration usually takes place during the night, but towards the end of the migration period smolts are also observed during the day (e.g., Osterdahl 1969; Thorpe and Morgan 1978). The fact that smolts move downstream at night may be an adaptation to avoid potential predators (Solomon 1982). At high latitudes in areas with midnight sun, Atlantic salmon and brown trout (*Salmo trutta*) smolts migrate during hours of strong sunlight (see Thorpe and Morgan 1978 for review). In a Swedish river at 64°N, Osterdahl (1969) observed a change from nocturnal migration in late May and early June to a diurnal pattern in late June. There was no information on the length of the night during the smolt run, but at this latitude in May and June the nights are short and there is no period of real darkness. Daytime migration may also occur farther south; in the River Piddle, U.K., many Atlantic salmon smolts migrated in bright sunlight, whereas brown trout smolts migrated primarily in the early hours of the night (Solomon 1978). Moreover, Fraser et al. (1993) maintained that late descending smolts tended to migrate during daytime because the higher water temperature increases their ability to avoid endothermic predators such as birds.

Temperature

Water temperature is one proximate factor initiating downstream migrations in fish (Jonsson 1991). Several studies have shown that increasing water temperature in the spring is strongly correlated with the initiation of the smolt run (e.g., White 1939; Mills 1964; Osterdahl 1969; Bagliniere 1976; Solomon 1978; Jonsson and Ruud-Hansen 1985). Several authors have reported that downstream migration of smolts of Atlantic salmon and brown trout occurs at about 10°C or slightly above (White 1939; Mills 1964; Osterdahl 1969; Solomon 1978). Jonsson and Ruud-Hansen (1985) reported that only water temperature, not water flow, turbidity, or lunar cycle influenced the timing of Atlantic salmon smolt migration in the River Imsa. The increase in water temperature between 9 April and 16 May explained 91, 95, and 89% of the yearly variance in the date of 25, 50, and 75% yearly cumulative smolt descent, respectively. Smolts began to descend at temperatures between 5.8–11.2°C and the smolt run started early in years when the water temperature was high or when the increase in temperature was rapid, indicating that for the River Imsa the timing of smolt descent was controlled by a combination of temperature and temperature increase during spring rather than by a specific water temperature or by degree-days. Direct experimental evidence would help determine whether these correlations are causally related to the initiation of smolt migration.

Water flow

High water flow in rivers may stimulate downstream movement in a large number of fish species (Jonsson 1991) and the downstream migration of smolts has been linked to increased water flow (e.g., Berry 1932, 1933; Allen 1944; Osterdahl 1969; Hesthagen and Gärnäs 1986). In the River Orkla, Norway, Hesthagen and Gärnäs (1986) observed that migration of Atlantic salmon smolts was initiated by the first spring peak in water discharge when the water temperature was above 2–3°C. It has been hypothesized that smolt migration is a result of a passive displacement (Tytler et al. 1978; Thorpe et al. 1981), although this hypothesis has gained little general support (Thorpe and Morgan 1978; Solomon 1978; Kennedy et al. 1984; Bourgeois and O'Connell 1988). It is clear, however, that smolts migrate more quickly at high water flow than low (Youngson et al. 1989). Smolts appear to move actively out into the main current of the river to avoid being caught in backwaters and sloughs (Hansen and Jonsson 1985), indicating that the descent is not purely passive. Similarly, smolts migrating through lakes move faster than the downstream current velocity (Groot 1965; Bourgeois and O'Connell 1988), suggesting that local adaptations in this trait may occur in salmonids reared above lakes (but see Thorpe et al. 1981 for evidence to the contrary). In both the rivers Gaula and Surna, the survival of hatchery-reared smolts improved significantly when they were released at high water discharge within the normal period of migration (Hvidsten and Hansen 1988), as was also observed in rivers in Maine, U.S.A. (Hosmer et al. 1979). This may be because they migrated at a faster speed and were closer to the water surface, using high turbitidy to make them less visible to predators.

Estuaries and fjords

Knowledge of salmonids in the early marine phase is relatively scarce and has been reviewed by Thorpe (1994). The estuarine residence time of Atlantic salmon is relatively brief, generally lasting only one or two tidal cycles (Tytler et al. 1978). In estuaries schools of postsmolts reside in and are displaced with the surface current and movement is influenced by the tide and the direction of the water flow (Carlin 1969; LaBar et al. 1978; Thorpe 1988; Pethon and Hansen 1990; Jonsson et al. 1993). Several authors have concluded that smolts in the upper estuary move by selective ebb tide transport (Fried et al. 1978; Moore et al. 1995) but display active swimming in the lower estuary or bays (Moore et al. 1995; Lacroix and McCurdy 1996). Tytler et al. (1978) found that hatchery fish spent less time in the estuary than wild fish, although the possibly greater effect of the stress of tagging on wild fish cannot be ruled out. The marine

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migration of Atlantic salmon has recently been reviewed by Hansen and Quinn (1998).

Olfactory imprinting

The differentiation of conspecific populations of Atlantic salmon and other salmonids, which makes their management complex, arises in part from their tendency to learn site-specific odors during freshwater residence and seaward migration and seek these odors when they mature years later. This homing behavior isolates populations which, under the pressure of natural selection in different habitats, adapt to their local environment (Saunders 1981; Taylor 1991). The patterns of olfactory learning that enable the salmon to home are thus critical aspects of their freshwater lives.

Although it is widely known that salmon usually return to their river of origin to spawn, two important issues remain unresolved for Atlantic salmon and their Pacific relatives. First, do salmon learn the site-specific odors at a single, critical period ("imprinting") or do they learn odors in sequence during all or part of their lives? Second, what is the interplay between homing and spawning site selection in determining the distribution of spawning adults? Both questions pertain to the spatial precision of homing, hence the potential for genetic isolation among progressively small local groups; however, only the first of these two issues will be discussed here.

Experimental studies on the spatial and temporal aspects of olfactory imprinting have generally taken one of two forms: displacement of salmon from their rearing site for release elsewhere and exposure of juvenile salmon to artificial odors at selected developmental stages. Displacement experiments, such as those conducted by Donaldson and Allen (1958) with coho salmon (*O. kisutch*), revealed that almost all salmon returned to their release site, not to the site where they were reared. Similar results have been obtained with Atlantic salmon (e.g., Carlin 1969; Potter and Russell 1994). Not only do salmon generally return to the river where they were released but they also tend to return to a particular section of the river rather than other sections (Atlantic salmon: Hvidsen et al. 1994; steelhead trout, *O. mykiss*: Wagner 1969; Cramer 1981). Atlantic salmon are particularly sensitive to olfactory learning during smolting (Morin et al. 1989*a*, 1989*b*). Salmonids exposed to morpholine or phenylethyl alcohol at the smolt stage were decoyed to sites containing the odor as mature adults (e.g., coho salmon, Scholz et al. 1976; steelhead trout, Scholz et al. 1978*a*; brown trout, Scholz et al. 1978*b*; Atlantic salmon, Sutterlin et al. 1982). Parr induced to undergo smolting by application of hormones imprinted on odors whereas controls did not (coho salmon, Hasler and Scholz 1983). Displacement, odor exposure, and hormone treatment studies all support the hypothesis that substantial imprinting occurs during the parr–smolt transformation.

Despite the large body of experimental evidence that olfactory imprinting takes place during smolting, other lines of evidence indicate that odors are learned much earlier and that homing is a more complex process (Riddell and Leggett 1981; reviewed by Dittman and Quinn 1996). First, many salmonids move away from their incubation site during their residence period in fresh water (as discussed above) and undergo smolt transformation farther down the river system, yet they home to natal sites, not to sites where they smolted. Second, close examination of the displacement studies reveals that when the release site is near the rearing site, many salmon return to the rearing site, especially if it is in the same river system (reviewed by Quinn 1993). Third, experiments have shown that salmon alevins and newly emerged fry learn and respond to the odors of a stream (Brannon 1972), conspecifics (Quinn and Hara 1986), and artificial substances (Courtenay 1989).

It has been hypothesized that salmon imprint or learn a sequence of odors during their period of freshwater residence and seaward migration (Harden Jones 1968; Brannon 1982) and that they reverse this sequence during their homing migration. This may explain why salmon displaced from their rearing sites as juveniles home to their release site as adults, especially if it is in a different drainage area than the rearing site. Once such salmon have located the release site, the rearing site is not detectable and there is no stimulus for further migration (Dittman and Quinn 1996). However, if they were able to detect odors experienced earlier in their lives as juveniles, they might continue migrating. The imprinting process, even at the smolt stage, seems to involve more than mere exposure to odors of a river or hatchery, as the date of release affects homing performance (Hansen and Jonsson 1991). In support of a sequential learning hypothesis, Hansen et al. (1983) have shown that smolts deprived of the experience of part of their migration route failed to return to their home river.

The act of migration itself may stimulate olfactory learning, as exposure to new odors can stimulate the thyroid hormones associated with smolt transformation and imprinting (Dittman and Quinn 1996). To the extent that this is true, salmon may learn new odors as often as their movements bring them into contact with such stimuli, although exposure to novel waters does not always increase thyroid hormone levels and successful imprinting does not depend on high or rapidly rising levels (Dittman et al. 1994).

Factors affecting smolt survival

The smolt window: physiology, behavior, and predation

Many factors affect smolt survival and return of adult salmon, although they are poorly known (e.g., Saunders 1981). Factors related to predation and processes in the open sea are beyond the scope of this paper and we will emphasize physiological factors operating at the parr–smolt transformation (smolting) and the postsmolt stage (the period just after the smolts have left the rivers). These periods are of particular interest in salmon ranching because they strongly influence overall marine survival (Thorpe 1994). The timing of smolt migration seems to be crucial for survival of Atlantic salmon (Hansen 1987) and the migratory timing of wild smolts is presumably an adaptation to the area's prevailing environmental conditions. When hatchery-reared salmon smolts are retained in fresh water they will "desmolt," losing many of the physiological and behavioral characteristics of smolts (Lundqvist and Fridberg 1982). (Desmolt may be an unfortunate term in that it implies a complete loss of smolt characters; although some critical aspects such as salinity tolerance and migratory urge are lost, elevated metabolic

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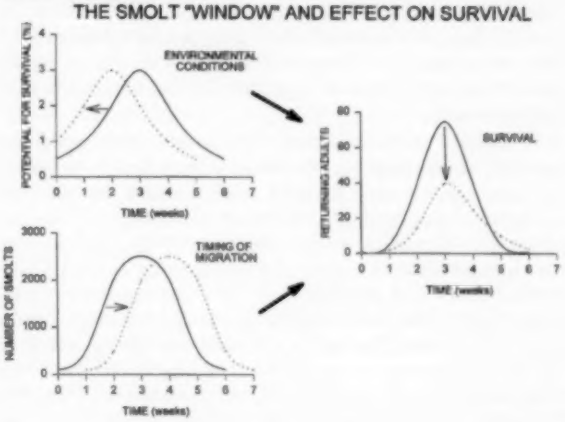
rate and scope for (freshwater) growth are not.) Duston et al. (1991) have shown that higher temperatures result in a more rapid loss of gill Na^+, K^+-ATPase activity and salinity tolerance. After analyzing data from several studies, McCormick et al. (1996) found that the decrease in gill Na^+, K^+-ATPase activity was directly related to the number of degree days (cumulative daily temperature) experienced by smolts; there is an 80% loss in enzyme activity (equivalent to parr levels) 400 degree-days after the peak in gill Na^+, K^+-ATPase activity. These results under controlled conditions indicate that the physiological smolt window will be narrower in warmer water. Recent work on the Connecticut River, which is near the historical southern limit of Atlantic salmon in North America, indicates that late migrants have lower gill Na^+, K^+-ATPase activity and salinity tolerance than early migrants and that increasing numbers of fish are affected in warmer years (S.D. McCormick, R.A. Cunjak, B. Dempson, M.F. O'Dea, and J.B. Carey, unpublished data). A temperature-related smolt window indicates that delays in migration (such as those that occur at dams) will decrease smolt survival and that these negative consequences will be greater in warmer, southern rivers.

In addition to the change in physiological state of smolts, it is likely that there are other mechanisms behind the observations that there is an optimal time for smolt migration. These are less well understood, but predators, diseases, parasite abundance, and food conditions clearly affect smolt survival. Atlantic salmon smolts are subjected to heavy predation (see Mather 1998) from birds such as gulls, cormorants, herons, and mergansers (Huntsman 1941; White 1957; Reitan et al. 1987; Kennedy and Greer 1988), and fishes such as Atlantic cod, saithe, pollack, striped bass, and sea trout (Hvidsten and Mokkelgjerd 1987). There may be an interaction between migration timing, physiological readiness, and predation. Under laboratory conditions the risk of predation is greater during acclimation of smolts to seawater and osmotic imbalance during seawater acclimation is greater in the presence of predators (Jarvi 1990; Handeland et al. 1997). Thus, even if smolts with reduced salinity tolerance (such as those migrating too early or too late in their development) survive when they enter seawater, they are less likely to escape predation due both to their greater susceptibility and the increased time they need to spend in an estuary for gradual acclimation. When smolts are retained in saltwater pens or cages from spring to late summer and autumn, they survive poorly when released despite their larger size (Hansen and Jonsson 1986, 1989). This is not the case, however, in Baltic salmon where experiments with delayed release have demonstrated greater survival from late summer and fall releases than spring releases (Eriksson 1988). Low salinity of the Baltic may release smolts from their normal dependence on spring increases in salinity tolerance.

These above findings indicate that there may be two interacting aspects of migration timing that affect smolt survival (Fig. 3). First, there is a physiological smolt window, controlled by photoperiod, temperature, and flow, that determines the physiological and behavioral readiness of smolt for migration and seawater entry. The importance of physiological readiness to survival is indicated by the correlation of adult return rates with the physiological condition of

Fig. 3. Simple mathematical model of the interaction of migration timing and environmental conditions and their effect on adult survival. Migration timing and survival estimates are typical for Atlantic salmon (e.g., Jonsson and Ruud-Hansen 1985; Hvidsten et al. 1995), but the temporal changes in environmental conditions are largely hypothetical. Values for migration timing are migrants per week. Adult returns are calculated from the weekly number of migrants and weekly survival rates. When migration timing and optimum environmental conditions coincide (solid lines), adult returns are high (total returns = 166). When migration timing and optimum environmental conditions are out of phase by 2 weeks (dashed lines), adult returns are lower (total returns = 94). Results of this simulation indicate that even when the magnitudes of migration and environmental conditions remain the same alterations in their timing can have significant effects on adult returns.



hatchery fish at the time of release (Virtanen et al. 1991; Staurnes et al. 1993). Second, there is an environmental smolt window, in which seasonal changes in environmental conditions in rivers, estuaries, and the coastal environment are appropriate for high smolt survival. In the simple population simulation shown in Fig. 3, when migration timing and optimum environmental conditions coincide, adult returns are high. When migration timing and optimum environmental conditions are out of phase, adult returns are substantially lower. Results of this hypothetical simulation indicate that even when the magnitudes of migration and environmental conditions remain the same, alterations in their timing can have significant effects on adult returns.

Pollution and stress

The physiological specializations that characterize smolts may make them susceptible to a variety of external stressors including pollutants. Although the greater capacity of smolts to respond to acute stress may be adaptive for migration and predator avoidance (Carey and McCormick 1998), it may have negative consequences under many natural and unnatural (anthropogenic) circumstances. One important example is the effect of acidity on smolt development. It has been known for some time that acid (and acid plus aluminum) exposures that have little effect on survival and growth of parr or smolts in fresh water can completely eliminate the

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development of gill Na^+, K^+-ATPase activity and salinity tolerance (Saunders et al. 1983). Recent work suggests that exposures as short as 12 h to relatively mild acidity (pH 5.2, 31 $\mu g L^{-1}$) aluminum) can compromise salinity tolerance (Staurnes et al. 1996*a*). The timing of exposure is also important; acid conditions that have little effect on smolts in April can greatly reduce salinity tolerance in May. Acid exposures at the smolt stage have devastating effects on adult return rates. Fish released in an acidic river in Norway often have no adult returns and have an average of one-tenth the returns of fish released at the mouth of the river or in a neighboring limed river (Staurnes et al. 1996*b*). These return rates were strongly correlated with the effect of acidity on gill Na^+, K^+-ATPase activity and osmotic balance of fish held in cages at the different release sites. These results illustrate two important points. First, the smolt stage may be particularly sensitive to acid rain (or run-off) and other pollutants. Second, by affecting the development of salinity tolerance, these detrimental effects may not be apparent until fish reach seawater. They may thus be difficult to distinguish from other marine mortality agents without experimental studies.

In addition to acidity, heavy metals and organic pollutants may also affect smolt development, although very few studies have specifically examined smolts. Heavy metals often exert lethal and sublethal effects on ion transport functions of the gill (Wendelaar Bonga and Lock 1992). Coho salmon are more sensitive to copper and zinc toxicity as smolts than as parr (Lorz and McPherson 1976). The numerous endocrine changes that occur during smolting may make smolts susceptible to environmental pollutants that act as endocrine disruptors (Kavlock et al. 1996). The smolt "habitats," the mainstem of rivers and estuaries, are more heavily impacted by pollutants than high elevation tributaries where fry and parr reside. The combination of potentially greater sensitivity of smolt and greater exposure to pollutants during migration may be important factors in smolt survival in many areas. Much more laboratory and field work needs to be done to examine the importance of pollutants in affecting migrating smolts.

Pollutants may also interfere with the development of olfactory imprinting by juveniles and its expression (homing by adults), though this has not been widely examined. Royce-Malmgren and Watson (1987) reported that the responses of juvenile Atlantic salmon to amino acids varied with pH and they hypothesized that straying might be greater in acidified rivers. We are not aware of evidence that straying and pollution are correlated and the olfactory imprinting process seems to be remarkably capable of separating ephemeral from essential chemical characteristics of rivers. Experiments and field data with Pacific salmon indicated that adults avoid contaminated water (e.g., by volcanic ash from Mt. St. Helens; Whitman et al. 1982; Leider 1989) but that adults exposed to pollution from ash or crude oil could subsequently home successfully in clean water (Whitman et al. 1982; Brannon et al. 1986).

Smolts are more sensitive to handling and swimming stresses than parr (Wendt and Saunders 1973; Carey and McCormick 1998). Although this may not be relevant for many wild populations, it may be important for hatchery smolts and smolts that must move over or around dams. The impact of handling at, or movement through, dam bypass structures or falling from great heights over dams has not been thoroughly examined. It is important to note that stresses may interact with one another or act additively to the detriment of smolt survival (Barton et al. 1986). As noted above, factors that may not be directly lethal (but have physiological effects) may increase susceptibility to predation.

Hatchery-rearing

Experiments carried out in the River Imsa show that the average survival rate of hatchery-reared smolts was only half that of wild fish (Jonsson et al. 1991). This deficit may be due to genetic changes related to the selection regimes in hatcheries and nature, behavioral differences induced by culture conditions, and differences in smolt quality (such as physical condition, physiological development, disease resistance, and coloration), and time and method of release. Survival may be 30 times higher in hatcheries than in nature, so inferior fish may survive in hatcheries that would have been culled in a river. Moreover, the physical fitness of hatchery fish at release may be lower than that of wild conspecifics. Poor fin condition is more frequent in hatchery populations than in the wild, but studies to date have yielded conflicting results as to the importance of fin condition to adult returns. Virtanen et al. (1991) and Vehanen et al. (1993) found no correlation between fin condition and return rate, whereas Farmer (1994) found that an index of smolt quality that included fin condition was correlated with return rates. Hatchery fish may also be at a disadvantage because of lower physical activity in hatchery tanks and ponds than in the wild. There may also be differences in timing of smolt development in hatchery fish that may be inherent in artificial rearing or related to specific hatchery conditions (e.g., photoperiod, temperature, and growth rate). The endocrine status of wild and hatchery fish can be very different (McCormick and Björnsson 1994), which in turn may affect the rate of physiological development, migratory timing, and return rates (Virtanen et al. 1991; Staurnes et al. 1993). Hatchery fish have little experience in catching natural food and avoiding predators but they may be able to learn very quickly (Stradmeyer and Thorpe 1987). Maynard et al. (1997) have recently reviewed hatchery performance in salmonid enhancement and concluded that "seminatural" culture conditions has the potential to increase smolt survival.

Summary and future research

Movement among habitats is very important in Atlantic salmon populations. There is no single sequence of movements that characterizes all populations from fry to smolts but rather there is an array of responses to the different environments of salmon populations. These include movements of fry from their redd sites, establishment and occupation of feeding territories, spawning movements of sexually mature male parr, shifting from summer feeding territories to winter habitat, descent of large parr from nursery streams to lower reaches of certain rivers in late autumn, and smolt migration

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in spring. Failure to protect these habitats and the capacity of fish to move freely among them may have detrimental effects on many populations.

Smolting is a highly adaptive specialization for downstream migration, seawater entry, and marine residence; it is controlled by several hormones and is characterized by numerous physiological and behavioral changes in fresh water which prepare smolts for an ocean existence. While still in fresh water, smolts become silvery and streamlined, lose their positive rheotactic behavior and territoriality and adopt downstream orientation and schooling tendencies, and undergo several physiological changes including increased salinity tolerance, metabolic rate, and scope for growth. Smolting is a critical stage for imprinting to odors used for homing, though some learning may also occur earlier. Photoperiod and, to some degree, temperature regulate physiological changes, whereas temperature and water flow seem to be key factors initiating downstream migration. The apparent existence of a smolt window may be due to a limited period of physiological and behavioral readiness of smolts for seaward migration and the timing of downstream movement into rivers, estuaries, and seawater with ecological conditions such as food resources and predators. Interaction among these factors is likely and makes both study and prediction of smolt mortality difficult.

Smolt development is adversely affected by acidity, unsuitable rearing conditions, and pollutants. In many cases (such as acid exposure) smolting is more sensitive than other life history stages. High temperature in spring will shorten the period of physiological preparedness of smolts. Unfortunately the migration habitat of smolts (the mainstems of rivers and their estuaries) are often the most heavily impacted by pollution, dams, temperature changes, altered hydrographs, and other anthropogenic changes. These factors may be directly lethal or may increase mortality rates by delaying or inhibiting smolt migration and making smolts more likely to encounter or be susceptible to predators.

The declines in Atlantic salmon populations in many geographic areas have made an increased understanding of salmon movement and migration imperative. Although salmon are well known for their accurate homing, they are also colonizers of previously uninhabited rivers and of new habitats within rivers systems. We currently have limited knowledge of the proximate factors (genetic and environmental) that regulate homing versus straying and the costs and rewards of exploring and colonizing new rivers or habitats within rivers. Are highly mobile individuals genetically different from the territorial residents? Are there stock-(river-)specific migratory traits and are these adaptive?

Atlantic salmon research should move toward a greater integration of physiology and behavior, which until recently have been examined separately. What are the environmental and neuroendocrine factors that initiate and maintain smolt migration and how do these relate to the physiological changes that occur during smolting? What are the energetic demands of migration and are they important to smolt survival? Is the altered growth pattern of mature parr the only factor affecting subsequent smolting or are there other mechanims by which maturation affects the individual's "decision" to smolt? What are the physiological triggers for movements of fry and parr in fresh water?

Human activity has dramatically affected salmon populations, particularly where industrial activity is high (Parrish et al. 1998). We do not yet know the factors that affect smolt survival during river, estuarine, and early ocean migration. How important are barriers to migration (such as dams) and pollution affecting smolt survival? Fisheries have altered the suites of predators in the coastal and ocean environment and these changes could significantly affect smolt survival. We have relied on laboratory experiments and hatchery-reared fish for much of our understanding of smolting and migration. We must know more about wild fish, understand the differences between hatchery and wild fish, and appreciate the potential impact of hatchery releases on wild fish.

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The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*)

Neil B. Metcalfe

Abstract: Atlantic salmon (*Salmo salar*) exhibit extreme diversity in the age of smolt migration and sexual maturation, both within and among populations. Theoretical analyses reveal the adaptive significance of such variation, but models of the underlying physiological and behavioral mechanisms are also needed. I summarize one such proximate model that suggests that smolting and maturation are only triggered if expected performance trajectories exceed threshold levels during sensitive periods. The probability of a threshold being exceeded is therefore dependent on an individual fish's ability to acquire and utilize resources efficiently, which in turn depends on a range of physiological and behavioral traits. Spatial variation in life histories is chiefly caused by differences in growth opportunity, although there is evidence of geographical variation in genetically determined expected growth trajectories. Simulations show that small changes in young fry growth rates can have pronounced effects on mean smolt age and sex ratio, by influencing the proportion of males that fail to exceed the threshold for early smolting and mature as parr (and so are less likely to survive to smolting). More sophisticated proximate models should allow powerful predictions of smolt production based on simple environmental parameters, due to their influence on growth trajectories and hence life history decisions.

Résumé : Chez le saumon de l'Atlantique (*Salmo salar*), on observe une très grande variabilité de l'âge de migration des smolts et de maturation sexuelle, dans les populations et entre les populations. Des analyses théoriques ont montré l'importance adaptative de cette variation, mais il faut aussi des modèles illustrant les mécanismes physiologiques et comportementaux sous-jacents. J'ai résumé un de ces modèles approximatifs qui semble indiquer que la smoltification et la maturation sont déclenchées seulement si les courbes de la performance prévue dépassent les valeurs seuils pendant les périodes sensibles. La probabilité de dépassement d'un seuil est donc dépendante de la capacité individuelle des poissons à acquérir et à utiliser les ressources de façon efficace, ce qui est fonction de divers traits physiologiques et comportementaux. La variation spatiale des cycles biologiques est principalement attribuable à des différences au niveau du potentiel de croissance, même en présence d'indications de variation géographique dans les courbes de croissance prévue déterminée par la génétique. Des simulations montrent que de faibles modifications du taux de croissance des alevins peuvent avoir des effets marqués sur l'âge moyen des smolts et le rapport de masculinité, en influant sur la proportion de mâles qui n'arrivent pas à dépasser la valeur seuil pour une smoltification précoce et qui atteignent la maturité à l'état de tacon (et qui ont moins de probabilité de survivre à la smoltification). Des modèles approximatifs plus perfectionnés devraient permettre des prévisions puissantes de la production de smolts fondées sur des paramètres environnementaux simples, en raison de leur influence sur les courbes de croissance et donc sur les décisions concernant le cycle biologique.

[Traduit par la Rédaction]

Introduction

Salmonids have received much attention from life history theoreticians so that there now exist many models of salmonid life histories which attempt to rationalize the observed variation in life history traits such as age–size at maturity or alternative reproductive strategies (e.g., Schaffer and Elson 1975; Bohlin et al. 1990; Hutchings and Myers 1994 and references therein). However, these are all ultimate models, in that they model the fitness consequences of alternative life history strategies, and it is essential to also look at the proximate mechanisms if we are to understand and predict how spatial and temporal variation in environmental conditions will influence the life history decisions reached by individual salmon. There has recently been an increasing interest in the link between causal and functional explanations of life history traits (e.g., Sinervo and Licht 1991); in this paper I aim to explore these issues in Atlantic salmon, *Salmo salar*, in particular concentrating on the interactions between physiological and behavioral parameters that trigger early life history decisions. The Atlantic salmon is an ideal species in which to study such effects: it exhibits extreme variation in life history strategies (see below) and it has been exceptionally well studied due to its economic and conservation value. Therefore, we are now in a position to begin relating the observed intraspecific variation in life histories to the underlying physiological mechanisms.

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N.B. Metcalfe. Fish Biology Group, Institute of Biomedical and Life Sciences, Graham Kerr Building, Glasgow University, Glasgow G12 8QQ, U.K.

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While some (usually male) Atlantic salmon remain and mature in their natal stream or river, the majority transform into the marine smolt stage and migrate downstream, entering the sea in the late spring (see McCormick et al. 1998). However, the age at which a fish undertakes this smolt migration varies both within and between rivers: smolts vary in age from 1 to 8 years old and single rivers often produce three or more age-classes of smolt (Metcalfe and Thorpe 1990). There is similar variation in age at first sexual maturation, with some males maturing at the end of their first summer while other fish only mature after having smolted and spent more than 2 years at sea (Thorpe 1994; Hutchings 1998). This life history variation is partly under environmental control, since the strategy an individual fish adopts is strongly influenced by the conditions it experiences (Thorpe et al. 1989; Rowe et al. 1991; Saunders et al. 1994; Berglund 1995; Friedland 1998; Hutchings 1998).

A proximate model for the triggering of life history events

It has long been recognized that there is a relationship between either event (smolt transformation, maturation) and body size, such that fish tend not to either smolt or mature until they have reached a certain size (Elson 1957; Myers et al. 1986). However, both smolt transformation and maturation take many months to complete: behavioral, physiological, and morphological indices indicate that under ambient conditions smolting is usually triggered about 7–10 months prior to entry to the sea (Thorpe 1977; Kristinsson et al. 1985; Metcalfe et al. 1986, 1988; Wright et al. 1990) while sexual maturation commences about a year prior to spawning (Simpson 1993; Thorpe 1994; Kadri et al. 1996; Stead 1996). During this intervening period the growth rates of the fish are influenced by the life history decision that they have taken: fish starting to either smolt or mature enter a phase of rapid growth compared to nonsmolting or immature individuals of the same age (Kristinsson et al. 1985; Metcalfe et al. 1988; Skilbrei 1988; Saunders et al. 1994; Kadri et al. 1996).

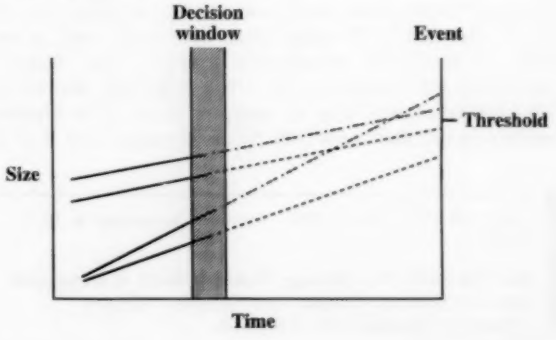
Therefore analyses of size at the time of spawning or entry to the sea tell us nothing about the underlying triggering mechanisms, since size by this stage is partly a consequence, rather than a cause, of the life history strategy that has been adopted. Models based on threshold size at this time (e.g., Power and Power 1994) do not therefore present a real picture of the life history decisions reached by the fish. We must instead examine the state of the fish at the time of the decision: what makes a fish begin the process of smolt transformation in late summer or maturation in late autumn? Current evidence (summarized in Thorpe et al. 1998) suggests that these events are triggered if the fish is on course to surpass a threshold state (cf. Roff 1996) by the time of entry to the sea or time of spawning, respectively. Thus smolt transformation is triggered in late summer if the fish is set to exceed a threshold size by the following spring, while maturation occurs if it is projected to exceed a threshold level of resources by the following autumn. In either case, the future state of the fish is presumably estimated from a combination of its current state and the rate at which that state is currently changing at the time of the life history decision. Therefore, in late summer the fish would be, in effect, estimating (from its current size and growth rate) what its size should be at the time of the smolt migration the following spring; if its projected size was above the genetically determined threshold then smolting would be triggered, while if it fell below the fish would remain as a parr in fresh water for a further year (Fig. 1; Thorpe et al. 1998). A similar process applies to maturation. The full model also incorporates other features such as the possibility for either process to be "switched off" if the fish's performance drops below expected levels during a second sensitive period a few months after the first.

This proximate life history model is simple, yet it captures the main elements of the extreme variation in observed life history patterns in Atlantic salmon. It does not imply that the fish make conscious assessments, decisions, or calculations, since all that is required is the evolution of simple rules of thumb (e.g., current size or growth rate could be approximated as concentrations or turnover rates of key metabolites, RNA synthesis rates etc., so that smolt transformation would only be triggered if these exceeded threshold levels during the sensitive period of the year). The approach is complementary to optimality models, since these indicate the reasons why smolting or maturation are inhibited if the projected state of the fish is subthreshold (because small smolts have a very poor survival rate (Lundqvist et al. 1994) and maturation at a small size is similarly prohibitively costly (Hutchings 1994)).

What determines whether fish achieve the trigger thresholds?

Put simply, fish must grow rapidly in order to surpass the thresholds that will trigger early smolting or maturation. It is therefore possible to predict spatial variation in these life history traits: at a population level the mean age of smolting is strongly negatively correlated with environmental indices of growth opportunity (based on degree-hours of daylight),

Fig. 1. The concept of thresholds determining life history decisions. Smolting or sexual maturation is only triggered if at the time of the sensitive window the state of the fish (e.g., its body size) is expected to exceed the relevant threshold by the time of the event (smolt migration or spawning). The sensitive window is many months prior to the event and so the projected trajectory is based on past/current performance. See text for further explanation.



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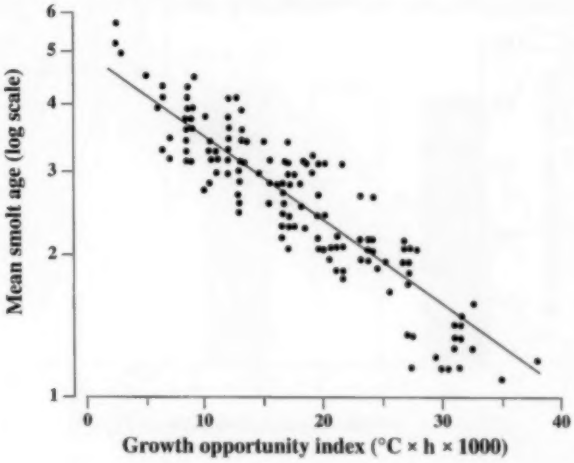
whether comparing between hatchery tanks (Thorpe et al. 1989) or rivers across the entire geographical range of the species (Fig. 2; Metcalfe and Thorpe 1990). Similarly, variation between populations in the incidence of early maturation is correlated with growth rates and (or) levels of energy reserves (Myers et al. 1986; Rowe and Thorpe 1990; Thorpe 1994; Berglund 1995). However, the pattern for early maturation is complicated by the fact that growth conditions in natural streams are rarely good enough to trigger maturation before the first opportunity for smolting; faster growing fish may become committed to smolt transformation, which removes them from the pool of fish available to mature the following year (see later). Within a single environment, an individual salmon's growth performance will be dependent on two factors: its ability to obtain resources and its ability to use them efficiently. Both involve the interaction between a combination of behavioral, ecological, and physiological parameters.

Individual variation in the ability to acquire resources

Food often appears to be limiting for salmon parr in the wild, as is evident from the fact that offspring of wild parents grow much faster in hatcheries than in the wild even under the same temperature and photoperiod regime. The amount of food available to a fish in a natural stream will be dependent on the quality of the feeding station(s) that it is able to obtain. Salmon parr are sit-and-wait predators that largely feed on invertebrates being carried past in the drift. Drift density is strongly correlated with local current velocity (Wankowski and Thorpe 1979; Fausch 1984) and so the complex bottom topography of salmon streams and rivers results in marked fine scale variation in the profitability of different potential feeding stations (Fausch 1984). The social structure of juvenile stream-living salmonids has been variously described as being strictly territorial (e.g., Kalleberg 1958) or based on a dominance hierarchy (e.g., Bachmann 1984); it is likely that the structure is a continuum dependent on density, with all fish taking up territories when the density is low but switching to a looser semishoaling distribution (with dominant fish in the hierarchy obtaining the better feeding positions) when the density of both food and fish is high (Wankowski and Thorpe 1979; Cutts 1996). Both territories and dominance hierarchies are relatively stable over time (Bachmann 1984; Abbott et al. 1985; Stradmeyer and Thorpe 1987) and so some fish will consistently be able to gain access to more food than others. Moreover, it is likely that those fish that do not obtain a feeding station during the early settlement period of the fry will be displaced downstream and will probably die either from starvation (Elliott 1994) or predation (Brännäs 1995).

The ability to obtain a good feeding station early in life is therefore of prime importance in determining future performance. Studies of first-feeding fry have revealed that success depends upon a combination of physiology and chance. In common with many other species (see Figler and Einhorn 1983; Beaugrand et al. 1996), prior ownership of a site is a strong factor influencing the outcome of territorial disputes: Cutts (1996) showed that salmon fry that had been resident on a territory for just 48 h were able to displace 75% of all

Fig. 2. The mean age of salmon smolts leaving a river is highly correlated (r^2 = 0.823) with an index of growth opportunity (monthly mean temperatures multiplied by hours of daylight). Relationship based on data from 182 rivers covering the entire geographical range of Atlantic salmon. (From Metcalfe and Thorpe 1990).



intruders of similar age; moreover, the larger fish of a pair won 92% of the time if it was the resident but only 38% if it was the intruder. As a result, early-emerging fish, which encounter an unoccupied habitat, tend to become established and survive better (in the absence of predation) than late fish (Mason and Chapman 1965; Chandler and Bjornn 1988). While prior ownership will to some extent be a chance effect, there are also intrinsic differences between fish that alter the likelihood of becoming established early. Not all fry will absorb their yolksac and begin feeding on exogenous food simultaneously — there is variation both within and between egg batches in the date of first feeding (Gustavson-Marjanen and Dowse 1983; Metcalfe and Thorpe 1992; Brännäs 1995). Variation between egg batches in the same stream is primarily due to different dates of spawning, but that within a batch of eggs has been shown in several species of salmonid to be linked to genetic differences between individuals: early-feeding salmonid fry tend to be more heterozygous (Allendorf et al. 1983; McCarthy et al. 1996), may be more likely to have a specific enzyme allele (e.g., PGM–1*r*b* in rainbow trout *Oncorhynchus mykiss*; Ferguson et al. 1987), and have higher than average standard metabolic rates (Metcalfe et al. 1995; Cutts 1996).

These intrinsic factors may also influence their level of aggressiveness and hence dominance status: salmon with high standard metabolic rates tend to be more aggressive (Cutts et al. 1998) and so become dominant (even after controlling for body size, date of first feeding, or prior residence) (Fig. 3; Metcalfe et al. 1995; Yamamoto et al. 1998). The PGM–1*r*b* allele in trout appears to have a similar effect (Ferguson and Danzmann 1985; Ferguson et al. 1987), possibly because it influences liver metabolism. The double advantage of a relatively high standard metabolic rate (i.e., a greater likelihood of both being a prior resident and being dominant) results in these fish tending to perform better,

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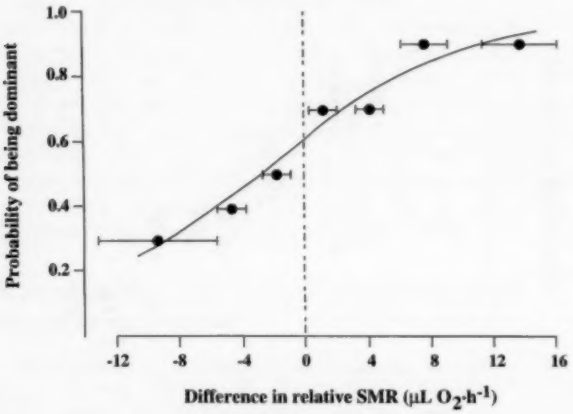
Fig. 3. The relationship between metabolic rate and dominance status. The probability of the earlier-feeding member of a pair of salmon fry being dominant over its opponent is shown relative to the difference in relative standard metabolic rate between the two fish; the fish with the relatively higher standard metabolic rate (SMR) (for its size) was significantly more likely to be dominant (based on 70 pairs; from Metcalfe et al. 1995).



both in terms of competition for feeding stations and subsequent growth. Evidence for this arises from the correlation between metabolic rate and otolith growth rate (Mosegaard et al. 1988; Wright 1991; Yamamoto et al. 1998): fish with larger otoliths at first feeding and hence presumed greater metabolic rates were more likely to obtain territories in a stream channel (Titus and Mosegaard 1991), survive in wild streams (Mosegaard 1990), and grow fast in the laboratory (Metcalfe et al. 1992). Other genetic differences between fish may also contribute to variation in aggressiveness and dominance and hence ability to obtain food. For instance, growth hormone (GH) affects aggressiveness as well as appetite, so that fish with enhanced GH levels tend to become more active and aggressive and so monopolize localized food sources (Johnsson and Björnsson 1994; Johnsson et al. 1996; Jönsson et al. 1998). It is therefore clear that several metabolic parameters influence the ability of salmonid fry to acquire resources, but as yet we do not know how they are interrelated. It is quite possible that natural individual variation in GH production, metabolic rate, and the expression of key enzyme alleles are all indices of the same general phenomenon, but these links have yet to be established.

Individual variation in the efficiency of resource utilization

All fish do not utilize their food with equal efficiency. Less is known about individual variability in resource use than in resource acquisition, but it is evident that both physiological and behavioral parameters influence growth efficiency. One of the few papers to investigate variation in physiological efficiency showed that there can be marked differences between similar-sized rainbow trout in the efficiency with which they convert a given amount of ingested protein into tissue and that these differences were chiefly due to variation in the rate at which existing body protein was being turned over: the fish that grew inefficiently did so because their protein degradation (and hence wastage) rates were high (McCarthy et al. 1994).

However, the cause of this variation in degradation rates is as yet unknown. One possibility is that degradation rates are influenced by social status, being higher in subordinates, since Abbott and Dill (1989) showed that subordinates grew slower than dominants even when both consumed equal rations. There are several possible physiological contributors to this effect, which are not mutually exclusive. (*i*) Subordinates might have to divert more resources into tissue repair as a result of injuries inflicted during encounters (see Abbott and Dill 1985; Christiansen et al. 1991). (*ii*) Their metabolic efficiency may be reduced due to the physiological stress of merely being in sight of a dominant (see Koebele (1985), although Huntingford et al. (1993) found no effect of visual exposure on feeding behavior in salmon). (*iii*) Their temporal pattern of feeding may be dictated by the need to avoid conflict with dominants and so may be suboptimal with respect to digestive efficiency (Alanärä and Brännäs 1997; Kadri et al. 1997). (*iv*) Spatial avoidance of dominant fish may lead to elevated levels of energy expenditure due to greater activity. The last possibility was highlighted in an analysis of energy budgets of stream-living rainbow trout of differing social status (Metcalfe 1986). In both dominant and subordinate fish there was a positive linear relationship between energy expenditure and food intake — fish had to expend energy (in holding position against the current, darting out to intercept and contest prey items etc.) in order to obtain food. However, the slope of the relationship (and hence the cost:benefit ratio) depended on social status, presumably because subordinates could not get access to any feeding stations that offered shelter against the current and so had to swim more actively. As a result, growth rates in subordinates were negatively correlated with food intake due to the excessive energy expenditure they incurred when attempting to feed at a high rate (Metcalfe 1986). It thus appeared that the optimal strategy (in terms of growth rate) for subordinates was to reduce energy expenditure to a minimum (by sheltering in the gravel substrate) rather than attempt to compete with dominants for feeding stations and food items in the areas of faster flowing water, despite the fact that the former strategy resulted in a reduced food intake rate. This may explain the existence of alternative behavioral strategies in juvenile salmonids: some fish do not attempt to hold territories, instead living either in the interstices between other territories or in nondefended areas and consequently reducing the amount of energy expended on competition, aggression, and territorial defence (Puckett and Dill 1985).

The costs and benefits of dominance

I have illustrated that parameters such as standard metabolic rate, growth hormone production, heterozygosity, and possibly key enzyme alleles such as PGM–1*r*b* may influence dominance status, which in turn affects the ability of the fish to both obtain resources and utilize them efficiently. While the initial relationship between body size and social status is weak (Huntingford et al. 1990; Metcalfe et al. 1992, 1995), the faster growth of dominant fish further consolidates their status through positive feedback. As a

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consequence, good competitors that establish their dominance in the first few weeks of life maintain a faster growth rate (Metcalfe et al. 1992) and are more likely to achieve the size threshold for early smolting (Metcalfe et al. 1989; Metcalfe 1991). Inevitably therefore there is a link between first feeding date within a cohort, early growth rate, and probability of early smolting (Fig. 4; Metcalfe and Thorpe 1992; McCarthy et al. 1996). Comparable data on the relationship between social status and timing of maturation are lacking, but it is likely that here too there is a direct connection, since early maturation in Atlantic salmon is triggered by rapid growth (Berglund 1992, 1995; Simpson 1992).

Therefore, why is there not continued selection for those traits that confer dominance, such as higher standard metabolic rate or levels of GH, or earlier emergence of fry? The reason seems to be that there are associated costs as well as benefits. Fish with relatively high standard metabolic rates have a greater "cost of living" — they must expend more energy simply in existence metabolism, so that at times of food shortage (or periods of suppressed appetite and energy conservation; Bull et al. 1996) they will utilize energy reserves faster, with a consequently greater risk of starvation. Moreover, their greater dominance status arises from being more aggressive and the energetic cost of this aggression may in some circumstances result in their growth rates being no faster than those of fish with lower metabolic rates (Cutts et al. 1998). Their behavior may also make them more vulnerable to predation: juvenile salmonids are most conspicuous to predators when actively foraging (Martel and Dill 1995) and may be targeted because of their reduced vigilance (Krause and Godin 1996) and fish with high levels of GH and consequently greater appetite maintain a higher level of feeding activity even after having experienced an attack from a predator (Jönsson et al. 1996). Aggressive fish may also experience a greater attack rate from predators due to decreased vigilance while fighting (Jakobsson et al. 1995). Moreover, the advantages of early fry emergence may again be offset by a greater predation risk. In general, territorial salmon may be less at risk from predators than floating or nonterritorial fish (Symons 1974). However, at the time of emergence the greater access to territories enjoyed by the earliest fry in a cohort to emerge is offset by a much higher risk of predation, since they gain none of the dilution advantages obtained by late-comers (Fig. 5; Brännäs 1995). Therefore, there is a balance between the competitive advantages enjoyed by intrinsically dominant fish and the associated survival costs.

Spatial variation in parameters influencing growth and development in wild fish

If there is a trade-off between the selection pressure for traits that confer dominance or competitiveness (and the associated higher feeding and growth rates) and that for traits that reduce predation risk and the risk of starvation, then we might expect the balance to vary with the nature of the environment. This should be revealed in terms of geographical variation in the frequencies of key alleles, especially those that influence metabolism. Perhaps the best evidence for this comes from studies of the Malic enzyme-2 (MEP-2*) locus. Fish that are heterozygous at this locus tend to mature earlier after having smolted (as grilse, after one winter at sea; Jordan et al. 1990). However, the relative frequency of the two alleles varies according to the local summer temperature regime, with MEP-2*(100) being predominant at warm sites but being almost completely replaced by MEP-2*(125) where the July temperature is 5°C or less; moreover, the same trend with temperature is found within single rivers in Scotland (Verspoor and Jordan 1989). This implies that the thermal regime imposes a selection pressure leading to locally optimal metabolic solutions.

The relationship documented in the laboratory between genetic variation in the regulatory gene PGM–1*r** and fish performance (e.g., Ferguson and Danzmann 1985; Ferguson et al. 1987) would lead to the prediction that there would be a similarly clear effect in the wild. However, Pollard et al. (1994) found no association between allelic variation at this locus and growth performance or smolt age in wild Atlantic salmon, although there was a very weak relationship across populations between the incidence of the PGM–1*r*b* allele

Fig. 4. Effect of first feeding date on early growth (expressed as mean forklength + S.E.). The earliest fish to feed within a single family of salmon fry were initially no larger than later-feeding sibs (top) but had established a clear size advantage three months later (bottom, from Metcalfe and Thorpe 1992).

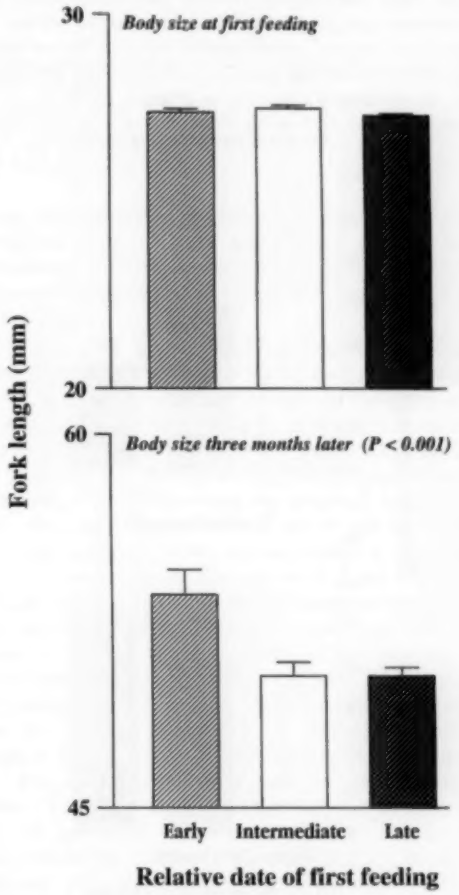

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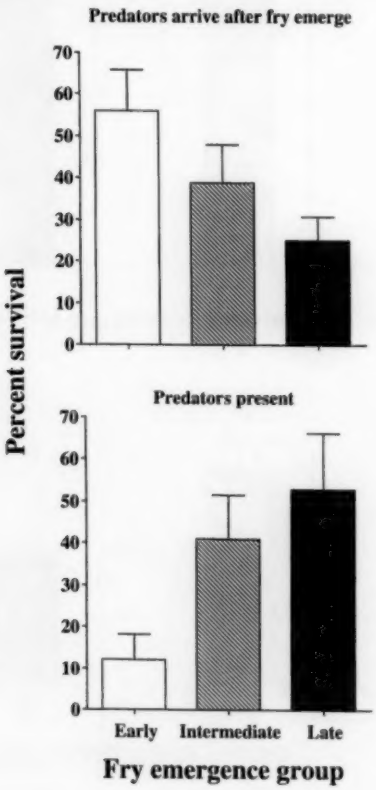
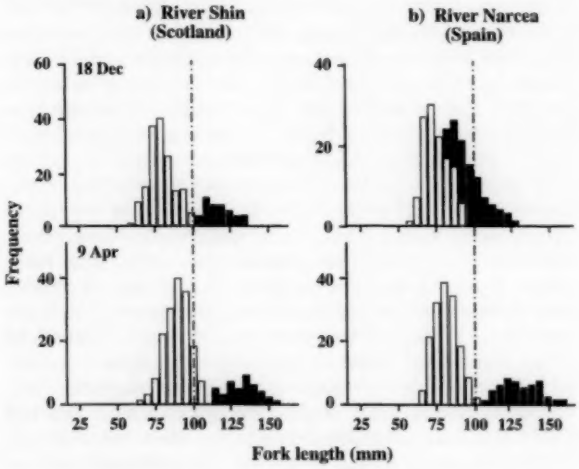
Fig. 5. The percentage of early, middle, and late-feeding salmon fry from the same family that survived in a simulated stream tank when a single predatory seatrout was released (top) 3 days after the "emergence" (= release) of the late-feeding fry and (bottom) before the emergence of the early-feeding fry. When predators arrive later, the early feeders gain the advantage of prior residence and greater local knowledge of the habitat, whereas when they are already present the early fry are exposed to a greater predation risk while late emerging fish gain the benefits of the dilution effect. From Brännäs (1995).



and the proportion of male parr that matured early. The lack of any stronger effect could just be due to the fact that all sampled fish were at least one year old (and in many cases were 3–4 years old); they were in effect the fittest fraction of the initial population, having survived the period of intense selection early in the first summer (Elliott 1994). All the less fit variants may thus have already been removed from the population, making it much harder to detect relationships between allelic variation and performance. This might also explain the similar lack of significant relationships between heterozygosity and performance in wild brook trout *Salvelinus fontinalis* (Hutchings and Ferguson 1992). Further genetic studies on wild fish are therefore needed at the very early life history stages, when selection pressures are probably at their greatest.

A second form of spatial variation in genetically determined life history parameters would be variation in the shape of the expected growth trajectory of the fish and

Fig. 6. Size frequency distributions of salmon from (a) the River Shin, Scotland and (b) the River Narcea, Spain, grown under the same conditions in a Spanish hatchery. Both populations showed the characteristic bimodal split into fish that would smolt aged 1+ (black bars) and those that would remain as parr until they were 2+ (white). The Scottish smolts initially grew faster and were on average significantly larger than the Spanish ones on 18 December (top graphs) but were smaller by the following 9 April due to showing negligible growth over winter (bottom graphs). These population differences in growth performance suggest local adaptations to anticipated seasonal variation in growth conditions. From Nicieza et al. (1994*a*).



hence the value of the life history thresholds (Thorpe et al. 1998). Nicieza et al. (1994*a*) pointed out that northern populations of salmon experience a more pronounced seasonal variation in growth opportunity than southern ones: fish in northern Spain are able to grow for at least 10 months of the year, whereas in northern Europe little growth may be possible from October to May. Therefore, fish should be adapted to this expected growth pattern so that northern salmon would have evolved a smolting size threshold that would assume much less growth from the timing of the decision through to smolt migration than would southern ones. Therefore the ratio of autumn size to spring (smolt) size should increase with latitude (Nicieza et al. 1994*a*). These predictions were tested by growing offspring of wild parents from the River Shin (northern Scotland, 58°N) and the River Narcea (Spain, 43°N) in the same hatchery in northern Spain. Shin salmon grew significantly faster than Narcea fish during the summer (Fig. 6), possibly due to their greater digestive rate (Nicieza et al. 1994*b*). However, the threshold size needed to trigger smolting was higher for these northern fish, so that the percentage of salmon that smolted after one year was in fact greatest in the Narcea population. Moreover, Shin fish showed a much greater reduction in growth rate over the winter (Fig. 6), so the Narcea fish were larger by the time of the actual migration (Nicieza et al. 1994*a*). This indicates that the fish show local adaptations to match typical environmental conditions: northern fish are apparently adapted to a climate where growth is normally only possible in summer, so that their metabolism may have evolved a greater

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Table 1. The relationships between body size (forklength (FL) in mm) at key times and the probability of smolting and sexual maturation in Atlantic salmon parr.

Date	Fish age	Life history event	x in logistic equation	Note
Late July	0+	P(will not smolt next spring)	$e^{41.818 - 0.862FL}$	(1)
Nov.	0+	P(male will mature at 1+)	$e^{0.3277FL - 21.684}$	(2)
June	2	P(Immature fish is now smolt)	$e^{0.0823FL - 9.8619}$	(3)
June	2	P(Previously mature male is now smolt)	$e^{0.0608FL - 9.3316}$	(4)

Note: In all cases the relationship is described by a logistic regression of the form $P(\text{event}) = x/(1 + x)$.
(1) From Metcalfe et al. (1989); $F = 14.92$, 1,59 d.f., $P < 0.001$. Equation calculated for fish of intermediate dominance status (rank = 5).
(2) From Simpson (1992); $F = 11.26$, 1,90 d.f., $P = 0.001$. Equation is for salmon in January, but there is negligible growth from November until then.
(3) Calculated from data in table II of Fängstam et al. (1993); Improvement $\chi^2 = 19.27$, 1 d.f., $P < 0.001$.
(4) Calculated from data in fig. 4 of Berglund et al. (1992); Improvement $\chi^2 = 13.43$, 1 d.f., $P < 0.001$.

seasonal fluctuation in scope, the fish adjusting their appetite in winter to the expected low availability of food (see Metcalfe et al. 1986; Bull et al. 1996; Simpson et al. 1996). In contrast, southern populations have evolved in a climate where growth can be maintained for most of the months leading up to the smolt migration, so smolting is triggered in fish that are still relatively small at the time of the life history decision in late summer.

Simulating the effect of environmental fluctuations on life history patterns

Elucidation of the proximate mechanisms that trigger life history decisions allows us to predict the outcome of changes in early growth performance, such as might be caused by annual fluctuations in summer temperatures or long-term changes in climate. While such simulation models are based on the decisions of individual fish, they allow us to predict changes at the population level, such as the mean age or sex ratio of the migrant smolts. Power and Power (1994) have produced a model that simulates these smolt parameters but it is based on observed mean values of the key parameters (such as size at smolting or proportion of males maturing), with no investigation of the underlying biological processes or causes of intraspecific variation. The model of Thorpe et al. (1998) is potentially very powerful in this respect but it has yet to be fully validated. I have therefore carried out some much simpler calculations based on size frequency distributions of a cohort of fish to show the scope of this kind of approach.

As outlined earlier, juvenile Atlantic salmon become committed to either smolting or nonsmolting in the summer preceding the spring migration, while sexual maturation is determined in November, a year ahead of spawning. We now have good data on the relationship between size of 0+ fish in July and the probability of smolting (Metcalfe et al. 1989), their size in November and the probability of male parr maturing (Simpson 1992), and their size as 2-year-old fish and the probability of smolting (separately for previously mature and immature parr; Berglund et al. 1992; Fängstam et al. 1993). Equations for these relationships are given in Table 1 and can be linked by information on growth trajectories between the relevant time points obtained from Thorpe et al. (1980) and Metcalfe et al. (1990). In addition we have information on survival rates in the field from a variety of studies. Myers (1984) provides some of the most relevant information since he calculates survival separately for maturing and immature fish. The mean proportion of 1+ parr surviving from one summer to the next was found to be 0.44 for immature fish and 0.27 for maturing males, while for 2+ parr the corresponding figures were 0.35 and 0.15 (Table 3 in Myers 1984).

These data come from a variety of sources and so caution must be used in interpreting the outcome of any simulations. However, it is clear that small changes in the initial growth rates of a cohort of fish can have dramatic effects on the mean age and sex ratio of the smolts, due to the effect on the initial smolting life history decision. Take a population of salmon living in conditions that are relatively favourable for growth, such that the mean size of the 0+ fish is 48 mm by July and the mean age of the migrant smolts is 1.3 years old (based on growth data in Metcalfe et al. 1989, 1990). Such conditions would be found in salmon rivers in southern England or northern France (Metcalfe and Thorpe 1990). The equations in Table 1, when coupled with the mortality rates detailed above, indicate that approximately 12.4% of males would mature at 1+ (Fig. 7a). This figure is relatively low, due to the fact that many fish are already committed to smolting at the earliest opportunity and so have left the river before their first opportunity to mature as parr. As a result, few males suffer the increased mortality cost of early maturation (Myers 1984) and the sex ratio of the smolts (males:females) is relatively balanced (0.93). However, if the growth conditions during just the first spring–summer are somewhat poorer than usual, so that the mean size of the 0+ fish by July is somewhat smaller, then many more will not be triggered to smolt at 1+; the mean smolt age will increase (Fig. 7b), many more of the males will then be set on course for maturing as parr and will therefore be more likely to die before being able to smolt, and so both the sex ratio of the smolts and the total smolt output will fall (Figs. 7c, 7d). Thus a 6.2% decrease in the mean size of 0+ fish in July (45 mm instead of 48 mm) is predicted to produce a mean smolt age of 1.83 instead of 1.34 and a sex ratio of 0.86 instead of 0.93 and overall smolt production will fall by about a third due to the greater chance of fish dying before they reach the smolt stage (Fig. 7). Conversely, an increased early growth rate would result in a decreased mean smolt age, increased smolt output, and more equal sex ratio.

The important aspect of these results is not the direction of the trends (since it is well known that smolt sex ratios are skewed in populations with high percentages of mature males, see Myers 1984) but the fact that large effects can be produced by short-lived changes in conditions: all of the

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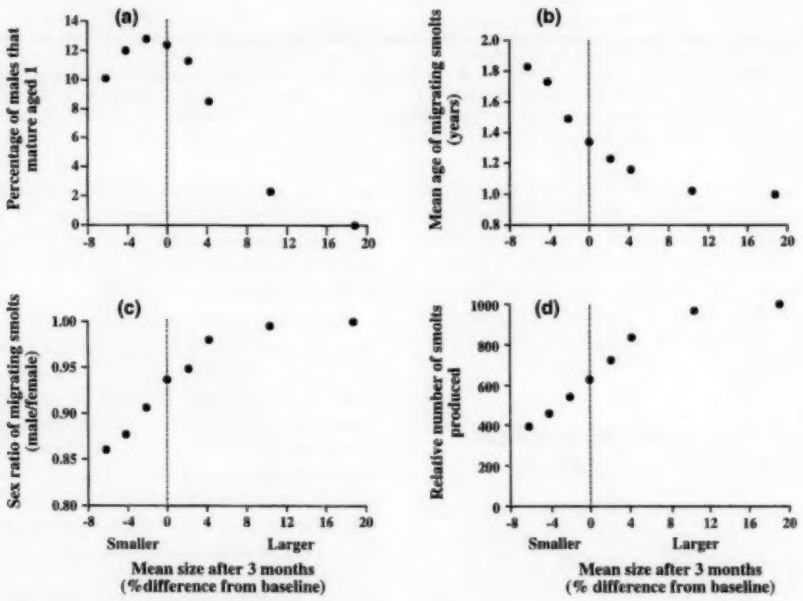
Fig. 7. Population responses predicted by the simulation model based on the relationships outlined in Table 1. In the baseline case the cohort of fry achieve a mean size of 48 mm by late July (3 months after first feeding). The graphs show responses to annual variation in early growth rates (mean size by late July being expressed as the percentage difference from the baseline, indicated by the dotted line). Responses shown are the percentage of males that become sexually mature parr at 1+, the mean age of smolts migrating to sea, the sex ratio of the smolts (males per female), and relative smolt production (expressed as the number of smolts that would be produced per 1000 year-old fish).



trends illustrated in Fig. 7 were produced by varying growth rates over just the first few months, since growth rates after the first July were similar in all simulation runs. Such large effects are produced because of the impact of changes in growth trajectories on the probabilities of individual fish attaining the thresholds needed to trigger these key life history events. The cascade effect of small variations in early growth may explain why it is extremely difficult to predict both spatial and temporal variation in smolt production when models ignore environmental parameters (such as temperature) that have a major effect on growth (Bradford et al. 1997). It should be noted, however, that the relative importance of growth rates during the first few months of life decreases as the mean smolt age of the population increases: in populations where none of the parr mature before they are 2+ or smolt before they are at least 3 then the impact of annual variation in growth rates during the first year of life is minimal except in that it may influence overwinter survival.

Conclusions

Models of the proximate mechanisms underlying alternative life history patterns are complementary to theoretical models of their adaptive significance. They also allow us to predict how changes in the environment will affect population structure. However, they are dependent on having a sound knowledge of the behavioral and physiological factors underlying the triggering of key life history events. In the case of Atlantic salmon, we now have enough behavioral and physiological information to create plausible if simple proximate models of the freshwater stages of the life cycle, covering the (alternative) processes of early sexual maturation and seaward migration.

This kind of modeling approach is clearly very powerful but it needs more detailed information. The major gaps in our knowledge are the relationships between parr body size and survival (both for mature and immature fish) and those between body size and smolting for older age-classes of parr; moreover we do not yet have extensive enough data to tell whether any of these relationships show marked and predictable geographical variation. While survival rates are known to be affected by initial density, it is also necessary to establish whether salmon parr exhibit density-dependent growth in the wild. However, such data are not impossible to collect and can be compared against sensitive growth models (see Elliott and Hurley 1997) and so it is realistic to suppose that we will soon be able to generate quantitative predictions of annual variation in smolt output and mature parr densities based on egg deposition rates and temperature profiles.

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The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon

L.P. Hansen and T.P. Quinn

Abstract: Atlantic salmon (*Salmo salar*) are distributed over large areas in the north Atlantic Ocean. They usually move very quickly from freshwater to oceanic areas, whereas there is considerable variation among Pacific salmon in early marine movements. In some areas, Atlantic salmon of exploitable size are sufficiently abundant that commercial high seas fisheries have developed. Such areas are off west Greenland, where North American and European fish are harvested, and in the Norwegian Sea, north of the Faroe Islands, where mainly European fish are exploited. Atlantic salmon feed on a wide range of large crustaceans, pelagic fish, and squid in the marine environment, supporting the hypothesis that Atlantic salmon are opportunistic feeders. In the ocean the salmon grow relatively quickly and the sea age when they become sexually mature depends on both genetics and on growing conditions. Natural marine mortality of salmon is highest during the first few months at sea and the major mortality factor is probably predation. However, marine mortality of Atlantic salmon has increased in recent years, apparently correlated with a decline in sea surface temperatures. Similar relationships between environmental conditions and the growth and survival of Pacific salmon have been reported. Atlantic salmon life histories most closely mimic stream-type chinook salmon or steelhead trout among the Pacific species. Finally, Atlantic and Pacific salmon return to their home rivers with high precision and possible mechanisms controlling the oceanic homing migration are presented and discussed.

Résumé : Le saumon de l'Atlantique (*Salmo salar*) est présent dans de grandes régions de l'Atlantique Nord. Il se déplace habituellement très rapidement depuis les eaux douces jusqu'aux régions océaniques, tandis que les déplacements en mer des jeunes saumons du Pacifique montrent une variation considérable. Dans certaines régions, le saumon atlantique de taille exploitable est suffisamment abondant pour permettre une pêche commerciale en haute mer. C'est le cas au large de la côte ouest du Groenland, où des poissons d'Amérique du Nord et d'Europe sont pêchés, et dans la mer de Norvège, au nord des îles Féroé, où ce sont principalement des poissons d'Europe qui sont exploités. Le saumon atlantique se nourrit dans le milieu marin d'un vaste éventail de gros crustacés, de poissons pélagiques et de calmars, ce qui va dans le sens de l'hypothèse selon laquelle le saumon atlantique serait opportuniste au chapitre de son alimentation. Le saumon croît relativement rapidement dans l'océan, et le nombre d'années en mer après lequel il atteint la maturité sexuelle dépend de facteurs génétiques et des conditions de croissance. La mortalité naturelle du saumon en mer est maximale durant les premiers mois qu'il passe dans ce milieu, et la cause principale de mortalité est probablement la prédation. Cependant, la mortalité en mer du saumon atlantique s'est accrue ces dernières années, observation qui est apparemment corrélée avec une baisse des températures de la surface de la mer. On a signalé des relations similaires entre les conditions environnementales et la croissance et la survie du saumon du Pacifique. Par comparaison avec les espèces du Pacifique, c'est aux cycles vitaux du saumon quinnat de type dulcicole et du saumon arc-en-ciel que ressemble le plus le cycle vital du saumon atlantique. Enfin, les saumons de l'Atlantique et du Pacifique reviennent dans leur rivière natale avec une grande précision; on présente et analyse des mécanismes qui pourraient régir cette migration océanique.

[Traduit par la Rédaction]

Introduction

Atlantic salmon (*Salmo salar*) are well known for their anadromous life history. Adults spawn in freshwater in the fall, the embryos incubate in gravel streambeds over the winter and emerge in spring as fry. They grow in freshwater as parr, often for 2–4 yr, before undergoing a transformation into seaward-migrating smolts. The post-smolts undertake a long journey in the ocean and as maturing adults salmon return with high precision to their natal river to spawn. Although anadromy is the most common life history pattern, resident individuals and populations of the species are well known, as in other salmonids (Jonsson and Jonsson 1993). Sexually mature male parr are common in many populations but in some populations no salmon go to sea (e.g., Mills 1989; Berg 1985). These populations may be landlocked, with a physical barrier to anadromy, but genetically distinct resident and anadromous populations can exist in sympatry (e.g., Verspoor and Cole 1989).

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L.P. Hansen[1]. Norwegian Institute for Nature Research, P.O. Box 736, Sentrum, N-0105 Oslo, Norway.
T.P. Quinn. School of Fisheries, Box 357980, University of Washington, Seattle, WA 98915 U.S.A.

[1]Author to whom all correspondence should be addressed. e-mail: l.p.hansen@ninaosl.ninaniku.no

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With the exception of such non-anadromous populations, Atlantic salmon are adapted to the prevailing environmental conditions that they encounter both in freshwater and at sea. The marine environment is a generalized one and the distributions of many populations overlap broadly. However, the surviving adult salmon almost invariably return to spawn in their natal stream (e.g., Malloch 1910; Carlin 1969; Swain 1982; Potter and Russell 1994; Youngson et al. 1994; reviewed by Quinn 1993) and the different regimes of natural selection in streams produce discrete populations, adapted to specific rivers, tributaries, or parts of rivers (e.g., Ståhl 1987; Hindar et al. 1991). The result of these adaptations is that, despite overlapping marine distributions, salmon spawned in different rivers vary in life history traits such as growth rate, age at sexual maturity, migration pattern and seasonal timing of return, frequency of mature male parr, resistance against diseases and parasites, survival rate in freshwater and at sea and time of spawning (e.g., Saunders 1981; Heggberget 1988; Bakke et al. 1990; Hansen and Jonsson 1991; Hindar et al. 1991; Taylor 1991). Salmon in different streams and rivers also differ in the frequencies of isozymes, which is indicative of reproductive isolation (Hindar et al. 1991).

The freshwater phases of the Atlantic salmon's life history and their habitat requirements have been extensively studied. In contrast, much less is known about their life at sea. Atlantic salmon are distributed over large areas in the north Atlantic Ocean during their migrations between freshwater and their feeding grounds at sea. They can be found from Connecticut to Ungava Bay in eastern North America and in Europe from northern Portugal to the border between Europe and Asia in northern Russia. Atlantic salmon are also present around the British Isles, Ireland, Iceland, and Greenland. In some oceanic areas (e.g., in the Norwegian Sea, north of the Faroe Islands, and between west Greenland and Labrador) the number of immature salmon has been sufficient to encourage commercial fisheries (e.g., Mills 1993). The brackish waters of the Baltic Sea also support a form of Atlantic salmon (called Baltic salmon) that only rarely moves into the Atlantic Ocean, but rather feeds in the southern Baltic Sea. Atlantic salmon may spend 1–5 yr in the ocean until they become sexually mature. Depending on the population and duration of marine residence, they may range from 1 to 30 kg.

Survival from smolt to adult varies considerably among stocks and years but is highest for salmon that have spent one winter at sea (known as grilse or one sea-winter [1 SW] fish). Many factors affect the marine survival of Atlantic salmon (Ritter 1989), although they are generally poorly understood (Friedland and Reddin 1993; Reddin and Friedland 1993). The parr–smolt transformation (smolting) and the post-smolt stage (the period just after the smolts have left the rivers) are of particular interest because these periods may be critical for survival in the sea (Browne et al. 1982).

In this paper we describe some important characteristics of Atlantic salmon during the marine phase of their life cycle: where the fish are distributed in time and space, what they eat, how fast they grow, and how long they stay in the sea before returning to freshwater to spawn. We also discuss migration and homing of salmon. These aspects of the marine life history of Atlantic salmon are compared with Pacific salmon (*Oncorhynchus* spp.) to better understand Atlantic salmon and to find common patterns and mechanisms.

Marine distribution

Atlantic salmon smolts leave fresh water and the post-smolts migrate to the feeding areas in the ocean during late spring and summer (e.g., Thorpe 1988; Mills 1989). When moving down rivers (Fried et al. 1978) and entering marine waters (Carlin 1969; McCleave 1978; LaBar et al. 1978; Holm et al. 1982; Jonsson et al. 1993), their movements seem to depend on the speed and direction of surface currents. Most of the records available suggest that post-smolts move relatively quickly into the ocean, swimming as fast as 2 body lengths·s^{-1} (Lacroix and McCurdy 1996), after a period of more passive movements with tidal currents. The duration of estuarine residence seems to be relatively brief. Further evidence, albeit indirect, of rapid migration comes from the fact that very few post-smolts are recorded in fjords and coastal waters during summer and autumn, although they are already present in oceanic areas in the east Atlantic (Holm et al. 1996; Holst et al. 1993, 1996; Shelton et al. 1997) and west Atlantic (Reddin and Short 1991) at this time of the year. However, Dutil and Coutu (1988) caught many post-smolts in a nearshore zone of the northern Gulf of St. Lawrence, suggesting that this trait may vary among populations or areas.

Studies of estuarine use by Pacific salmon reveal considerable variation among species, confounding any simple comparison with Atlantic salmon (reviewed by Thorpe 1994). Chum salmon (*O. keta*) and underyearling (ocean-type) chinook salmon (*O. tshawytscha*) seem to rely more heavily on estuaries than the other species (Healey 1982*a*; Simenstad et al. 1982). The species that are larger at seawater entry owing to longer freshwater residence periods (steelhead trout, *O. mykiss*; sockeye salmon, *O. nerka*; coho salmon, *O. kisutch*; and yearling (stream-type) chinook salmon) seem to migrate more rapidly through estuaries and occupy pelagic rather than littoral habitats, in comparison to the other species or life history types (McCabe et al. 1983). This trend is consistent with the limited use of estuaries by Atlantic salmon, as they are relatively large as smolts.

There is considerable variation among Pacific salmon in early marine movements as well as estuary use. Sockeye, chum, and pink (*O. gorbuscha*) salmon move relatively rapidly through coastal waters (Hartt and Dell 1986; e.g., sockeye: Straty 1981; Groot et al. 1989) whereas coho and chinook salmon have a greater tendency to remain in coastal waters (Miller et al. 1983; Healey and Groot 1987; Pearcy and Fisher 1988). Among chinook salmon, this coastal distribution is particularly pronounced among ocean-type populations — those that migrate to sea as juveniles in their first year of life. Stream-type chinook (those that rear for a full year or more in freshwater prior to seaward migration) more commonly migrate to the open ocean (Healey 1983). Steelhead trout move quickly through estuaries (McCabe et al. 1983) and out to the open sea for several years (Burgner et al. 1992) whereas their closest relative, the cutthroat trout (*O. clarki*), seems to spend only the summer at sea (Pearcy et al. 1990). The complexity of patterns within the Pacific salmon preclude any simple comparison with Atlantic

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salmon but the marine movements of Atlantic salmon seem to resemble those of sockeye or stream-type chinook salmon more than the other Pacific species.

A number of post-smolts have been caught in oceanic areas of the northeast Atlantic in recent years during pelagic trawl surveys in the Norwegian Sea in July and August (Holm et al. 1996; Holst et al. 1993, 1996) and north of Scotland in May and June (Holm et al. 1996; Holst et al. 1996; Shelton et al. 1997). Based on the distribution of catches north of Scotland, the fish appeared to move northwards with the shelf edge current (Shelton et al. 1997). Farther north in the Norwegian Sea post-smolts were caught beyond 70°N in July. Analysis of growth and smolt age distribution strongly suggested that most of the post-smolts originated from rivers in southern Europe (Holst et al. 1996). This was supported by the recapture of a salmon that had been tagged in April 1995 in southern England and recovered about 2000 km farther north three months later, demonstrating the capacity for rapid travel by post-smolts (Holst et al. 1996).

In the Labrador Sea, Reddin and Short (1991) caught many post-smolts in the early autumn of 1987 and 1988, using surface drift nets. The highest catch rates occurred between 56 and 58°N and they also caught many older salmon in the area. Based on age analysis, they concluded that post-smolts originating from Maine to Labrador were present. This was supported by recoveries of two post-smolts that had been tagged in the Penobscot River in Maine and Western Arm Brook, Newfoundland. In addition, four older fish in the Labrador Sea had tags, three from the Penobscot River and one from the Middle River, Nova Scotia.

When Atlantic salmon have reached catchable size, their marine distribution is easier to document. Many countries have had major tagging programs on smolts and adults and some of these fish have been recaptured in the high seas fisheries. It is difficult to know the true distribution of salmon at sea, as recoveries depend on the distribution of fishing effort. The absence of fishing pressure in an area does not demonstrate the absence of salmon, although one may assume that there is at least some general correspondence between the distributions of fish and fishermen. The waters off the western coast of Greenland contain many immature salmon that have spent one winter at sea (one sea winter or 1SW) or more than one winter at sea (multi-sea winter or MSW fish). Here, fish from both North America and Europe feed during June–September and are exploited.

Several studies have been carried out to assess the composition of the stocks present in the west Greenland area and establish the origin of these fish (e.g., Parrish and Horsted 1980; Reddin 1988). Swain (1980) analyzed a time series of smolt taggings in European rivers in relation to recaptures off west Greenland as Ruggles and Ritter (1980) did for North American smolt taggings. Møller Jensen (1980*a*) used tag recoveries from west Greenland in 1972 to assess the distribution along the west Greenland coast of salmon origination from North America and Europe. These investigations showed that Atlantic salmon from a number of different rivers in North America and Europe were present in the area. Furthermore, based on much more comprehensive material, Reddin (1988) and Reddin et al. (1988) used a discriminant analysis of scale characteristics and concluded that catches of salmon off west Greenland are split fairly evenly between the two continents. It is more difficult to determine the country of origin, but Canada apparently accounts for most of the North American component and Scotland accounts for most of the European fish (Møller Jensen 1980*a*). All in all, salmon tagged as smolts in home waters and recaptured at west Greenland have originated from Canada, U.S.A., Scotland, England, France, Norway, Sweden, Iceland, and Ireland, and some Russian salmon may also be present in the area.

At the end of the 1960s and beginning of 1970s, tagging experiments took place off west Greenland (Møller Jensen 1980*b*). In total 4657 salmon were tagged and 93 fish were recaptured outside Greenland: 28 in North America and 65 in Europe. The tags were reported from the United Kingdom (44), Canada (28), Ireland (16), Spain (3), and France (2). Taking into account the production of smolts in these countries, this suggests that larger proportions of salmon from more southern areas of Europe are present in this area than from farther north.

In the east Atlantic, salmon are found in large areas in the Norwegian Sea. In the 1970s there was an important commercial longline fishery far north in the Norwegian Sea in February–May. Recoveries of fish in this fishery that had been tagged as smolts and recaptures in coastal and freshwater fisheries of salmon tagged in the Norwegian Sea suggested that Norwegian salmon were most abundant, although fish from the United Kingdom, Sweden, and Russia were also present. Most of the fish were recaptured in homewaters the same year that they were tagged, suggesting that they were maturing (Rosseland 1971). Towards the end of the 1970s, fishing for salmon in the northern Norwegian Sea was banned and fishing was limited to the area within the Faroese Exclusive Economic Zone (EEZ).

The abundance of salmon within the Faroese EEZ has been assessed from sampling the fishery for a number of years. Jakupsstovu (1988) reported on a tagging program at sea from 1969 to 1976 in which 1946 salmon caught on longlines were tagged and released. The fish were tagged in more southerly areas of the Faroes and 1SW fish were probably highly overrepresented. In total, 90 fish were recovered, 33 in Scotland, 31 in Norway, 15 in Ireland, 8 in other European countries, and 3 at west Greenland. The great majority of the tags were reported in homewaters the same year they were tagged. However, it is interesting to note that some fish in the area may have been on their way westwards, as they were reported from west Greenland later that year.

In recent years a tagging program has been carried out in the major fishing grounds north of the Faroes. From November to March in the 1992/93, 1993/94, and 1994/95 fishing seasons, 5448 salmon were caught by longline, tagged, and released (Hansen and Jacobsen 1997). To date, slightly over 100 fish have been recaptured and preliminary results suggest that Norwegian salmon were most abundant in the area but Scottish and Russian salmon were also common. Some additional recaptures were reported from Ireland, Iceland, Spain, Sweden, Denmark, England, and even Canada.

Like Atlantic salmon, Pacific salmon have been subjected to mixed stock fishing for several decades. A variety of techniques have been used to describe the distribution patterns of the species and major stock complexes, including coded

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wire, disk and spaghetti tags, analysis of natural variation in parasite faunas, scale patterns, and isozymes. Reports for each species have been published as bulletins of the International North Pacific Fisheries Commission, which has been replaced by the North Pacific Anadromous Fisheries Commission (coho: Godfrey et al. 1975; sockeye: French et al. 1976; chum: Neave et al. 1976; chinook: Major et al. 1978; pink: Takagi et al. 1981; steelhead: Burgner et al. 1992). In general, sockeye, chum, and pink salmon and steelhead trout (at least from North America) are almost exclusively distributed in offshore waters, whereas many coho and chinook populations remain near the coast. There is considerable mixing of species and populations and fish from both continents (North America and Asia) can be found in some of the same oceanic areas.

The distribution of Atlantic salmon in the ocean is still not well known but the limited information indicates that salmon are not evenly distributed. Salmon from North America seem to stay in the west Atlantic area, although some fish can move into the northeast Atlantic. It is also evident that a relatively large proportion of the European MSW salmon moves far into the west Atlantic to feed. Salmon from many populations differ in how long the fish stay at sea; hence different sea age-classes from the same populations may be present in different areas. For example, MSW salmon may move farther away from home than grilse. The distribution of Atlantic salmon in the sea seems to reflect environmental factors such as surface temperature and surface currents (Reddin and Shearer 1987; Reddin and Friedland 1993) and probably also the availability of suitable food organisms, as growth and survival are important fitness characters as well. Likewise, the marine distributions of Pacific salmon are apparently influenced by a combination of temperature and food availability as would be predicted from the basic principles of bioenergetics (Welch et al. 1995; Rand et al. 1997). There may also be genetically determined, population-specific migration patterns as suggested for Pacific salmon (Brannon 1984; Pascual and Quinn 1994). The environmental factors are not only proximate stimuli that may affect migration but they are also part of the selection regime that gave rise to the genetic tendencies to migrate to certain locations.

Data compiled by Beamish and Bouillon (1993) indicated that the long-term annual catch of Pacific salmon is 556 000 t. For comparison, the total annual reported catch of Atlantic salmon has declined from about 6500 t in 1988 to 2300 t in 1997 (ICES 1998). The relative abundance of the Pacific salmon species (by weight) is pink (42.7%), chum (29.2%), sockeye (17.4%), coho (6.6%), and chinook (4.2%). Given their small body size, pink salmon abundance would be much greater if reported in terms of individual fish. The relative abundance of the species in North America (as opposed to Asia, based on the nation whose fishery caught the fish) has been less than half for chum (31%) and pink (41.3%), but more than half for sockeye (73.6%), coho (74.3%), and chinook (89.6%). Comparable records were not reported for steelhead and cutthroat trout, but they are much less abundant than the other Pacific species. The abundance of Atlantic salmon might be most comparable to that of steelhead.

In addition to the wild Atlantic salmon, there has been a great increase in the abundance of hatchery-reared fish in recent years. In Iceland, major sea ranching programs have been carried out and the total catch is significant when compared with that of wild fish (Isaksson 1988). In several countries, especially Norway and Scotland, a huge salmon farming industry has also developed. Escaped farm fish have been observed in several areas in the northeast Atlantic and they contribute substantially to salmon fisheries in Norway and the Faroes. In Norway, recent estimates suggested that nearly 50% of the salmon catch in coastal bagnets were escaped farmed fish (Lund et al. 1996) and an estimate from Faroes in the 1990/91 fishing season suggested that 40–50% of the catch were farmed fish (Hansen et al. 1993*a*). However, at west Greenland, the incidence of farmed fish appeared to be very small (Hansen et al. 1997). The behavior and life history of these farmed fish in the ocean is virtually unknown.

Food habits

Although more information about Atlantic salmon in the marine phase has been generated in recent years (e.g., Mills 1993), little is known about their food and feeding habits in the ocean. Salmon spend most of their time in the ocean close to the surface and prey on different pelagic animals like crustaceans, fish, and squid. Several authors have suggested that Atlantic salmon are opportunistic feeders (Hansen and Pethon 1985; Reddin 1988; Hislop and Shelton 1993) but there is no information available to compare the diet of salmon with the distribution of available food organisms. Hislop and Shelton (1993) summarized the prey of Atlantic salmon in the sea and concluded that small post-smolts fed mainly on invertebrates including terrestrial insects but fish predominated in the diet of larger salmon. They also concluded that the species of fish eaten varied between areas and years and suggested that salmon abundance is unlikely to be sensitive to year-to-year changes in any particular prey. Morgan et al. (1986) reported that 21 post-smolts, caught shortly after emigration from the rivers into the Firth of Clyde, west Scotland, had eaten principally sandeels, *Ammodytes* sp. In July, the main food items of post-smolts in the northern Gulf of St. Lawrence were invertebrates (Insecta, mainly Chironomidae and Crustacea, mainly Gammaridae; Dutil and Coutu 1988). Later in the summer and autumn, the post-smolts consumed mainly small fish, especially sandeels, *Ammodytes americanus*. Capelin, *Mallotus villosus*, were also relatively common prey and euphausids were the most frequently eaten crustaceans.

Levings et al. (1994) and Hvidsten et al. (1995) caught post-smolts by pair-trawling at different sites in Trondheimsfjord, Norway in May and June, 1992–1994. These fish may have been at sea for a few days to a few weeks. In the estuary, the stomach contents were dominated by prey taken in the river (Levings et al. 1994), whereas prey species occurring in brackish and salt water were found in stomach samples collected farther out. There was great variation in the prey among the years. For example, in 1992 the dominant prey was insects whereas in 1994 it was crustaceans.

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Still farther out in the fjord, the dominant food group was euphausids, whereas at the fjord mouth amphipods (Hyperiidae) and fish (herring, *Clupea harengus*, larvae) were more abundant. Ranched post-smolts in coastal waters of west Iceland in 1989 and 1990 had eaten primarily crab larvae, amphipods, copepods, and diptera imagos (Sturlaugsson 1994).

There is some information about feeding of immature salmon in the ocean (reviewed by Reddin 1988; Hislop and Shelton 1993). In the northwest Atlantic, salmon feed mainly on capelin, sandeels, amphipods, and euphausids (Templeman 1968; Lear 1980; Reddin 1985). In the northeast Atlantic, salmon feed mainly on herring, lantern fish (Myctophidae), sandeels, amphipods, and euphausids (e.g., Thurow 1973; Hislop and Youngson 1984; Hansen and Pethon 1985). The Institute of Marine Research in Bergen, Norway, caught salmon in pelagic trawl surveys for marine species in the Norwegian Sea during the summers of 1991 and 1995 and off the Hebrides in 1995 (Holst et al. 1996). The main fish species identified in the trawl catches were herring, mackerel, *Scomber scombrus*, lumpsucker, *Cyclopterus lumpus*, and Atlantic salmon. In total, 34 post-smolts were caught in 1991 and 108 in 1995. In the Norwegian sea, the most common prey observed in post-smolts were amphipods (*Themisto* spp.), krill (Euphausidae), herring and redfish, *Sebastes* spp., larvae, whereas off the Hebrides blue whiting, *Micromesistius poutassou*, larvae were the only food item identified.

The food of salmon has recently been examined from samples taken in a research fishery north of the Faroe Islands (Jacobsen and Hansen 1996). The stomachs of 3848 salmon, caught with longline baited with sprat, *Sprattus sprattus*, between November and March of 1992/93, 1993/94, and 1994/95, were examined. Crustaceans such as *Themisto* spp., euphausids, and shrimps accounted for more than 80% of the diet by count but by weight more that 60% of the stomach contents were fish, particularly lantern fishes, pearlside, *Maurolicus muelleri*, and barracudinas, (Paralepididae). Some herring, blue whiting, and mackerel were also observed.

During the homeward migration the feeding activity of Atlantic salmon tends to cease and a large sampling from bagnet fisheries in Norwegian home waters revealed that only about 10% of the stomachs contained food (Hansen and Pethon, unpublished data). Of those that had eaten recently, fish were by far the most abundant prey, especially herring, sprat, and sandeels. This tendency to eat fish is consistent with other studies. Grønvik and Klemetsen (1987) reported that herring were the most important prey in a small number of adult salmon examined in a fjord in northern Norway and salmon caught in bagnets on the Scottish west coast had eaten mainly sandeels (Fraser 1987). Fraser's (1987) results indicated that salmon were feeding until June or early July; thereafter all salmon stomachs he examined were empty. Hislop and Webb (1992) examined the stomachs of 54 salmon escaped from fish farms and found that 35% contained food, primarily juvenile whiting.

It is difficult to draw strict comparisons between the diets of Atlantic and Pacific salmon species because the available prey are different and because so many other factors affect diet analysis, including location (habitat and depth), timing (time of day, season, and year), predator size, and maturity state, etc. Bearing these complications in mind, the fish-oriented diet of Atlantic salmon seems most comparable to that of chinook among the Pacific salmon species, based on stomach contents (e.g., Beacham 1986) and analysis of stable isotopes (Welch and Parsons 1993). However, considerable overlap exists among most Pacific salmon species (e.g., Tadokoro et al. 1996). Brodeur (1990) reviewed the literature on Pacific salmon diets and reached the following conclusion. Sockeye and pink salmon subsist mainly on small zooplankton but will consume small nekton (fishes and squids) especially at a larger size. Chum salmon generally consume small crustaceans but often consume pteropods and gelatinous species and their diet is most distinctive among all the salmonids. Coho salmon and steelhead trout exhibit a mixed diet of fish and invertebrates. Masu and chinook salmon and cutthroat trout are mainly piscivorous in all phases of their marine existence.

Growth and maturity

In the ocean, Atlantic and Pacific salmon grow relatively quickly. The plasticity of salmon growth makes determining the extent of genetic and environmental influences difficult (Thorpe and Stradmeyer 1995). Differences in growth rates could, for example, be due to variable food supply or more general changes in oceanographic processes and structural features in the water column (Levings 1994). These changes might affect some populations more than others, depending on their marine distribution. Differences in growth rates may also be shaped by patterns of natural selection in individual rivers. Jonsson et al. (1991) observed that Atlantic salmon in rivers with annual average flows of less than 40 $m^3 \cdot s^{-1}$ were smaller than salmon in larger rivers and suggested that selection in small rivers may act against large salmon because low water flows make successful ascent and breeding by large salmon risky and difficult. Rogers (1987*a*) also pointed out that sockeye salmon spawning in shallow streams within the Wood River lake system are younger and smaller bodied than are the salmon spawning in larger rivers. He hypothesized that access to the shallow streams may have selected against larger individuals but pointed out that selective predation by bears on larger salmon in small streams might also influence the evolution of size and age at maturity.

Although there is no direct evidence of density-dependent growth of Atlantic salmon in the marine environment, evidence has been accumulating for some time that the Pacific Ocean's capacity to grow salmon is not limitless. Rogers (1980) and Peterman (1984) presented evidence of density-dependent marine growth of sockeye salmon. Although there is considerable population-specific variation in age structure and size at age within species (e.g., chum: Beacham and Murray 1987; pink: Beacham et al. 1988; sockeye: Blair et al. 1993; chinook: Roni and Quinn 1995), interannual variation in these linked traits seems to reflect growing conditions at sea. Poor growth is associated with delayed maturation, hence higher mean age, but smaller size at age (Ishida et al. 1993; Rogers and Ruggerone 1993), and ocean temperatures have been correlated with age at maturation

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(e.g., Blackbourn 1987*a*). It appears that, at least for some stock complexes such as Bristol Bay sockeye salmon, the density-dependent growth pattern has changed in the last 20 yr. Large runs of salmon are still associated with smaller body size than smaller runs but the salmon are now larger than before at a given density (Rogers and Ruggerone 1993, and D. Rogers, University of Washington, unpublished data). The good growth at sea since the late 1970s is positively correlated with water termperature (Rogers and Ruggerone 1993) and is consistent with the relatively high abundance of zooplankton in the Gulf of Alaska during the recent period of high salmon abundance (Brodeur and Ware 1992). The density-dependent effect is seen primarily in the final months at sea, when the large numbers of salmon are becoming more concentrated as they approach Bristol Bay.

In recent years a significant decline in the abundance of Atlantic salmon has been observed over most of their distribution range. The decline has been most pronounced in MSW salmon (ICES 1996). Possible explanations for this change have been proposed, ranging from changes in the ocean climate (Friedland et al. 1993; Friedland 1998) to effects of selective harvesting (Shaeffer and Elson 1975). Likewise, the past few years have greatly increased interest in decreasing body size and increased age among Pacific salmon populations (Rogers and Ruggerone 1993; McKinnell 1995; Bigler et al. 1996) and trends in abundance (McKinnell 1995; Beamish and Bouillon 1993; Beamish 1994; Hare and Francis 1995). There have also been concerns about the effects of possible future climate change on ocean conditions important to salmon (e.g., Hinch et al. 1995) and considerable effort is being devoted to understanding the links between climate, physical conditions in the ocean (e.g., upwelling, temperature, salinity, circulation), primary and secondary production, and the growth and survival of salmon.

Marine mortality

Survival of Atlantic salmon smolts to adulthood varies greatly among years and stocks. Marine survival rate of salmon has been estimated at 30–40% for wild salmon from the River Bush, Northern Ireland (Crozier and Kennedy 1993). Similar figures have also been observed in salmon from the River North Esk in Scotland (Shearer 1992). These observations have been made in years when survival rates were high. On the other hand, marine survival rates of salmon can be less than 5%. Several factors may affect the survival of salmon in the sea, including disease, predation, and food resources. Even though a number of different diseases and parasites affecting salmon have been described from the wild, in hatcheries and fish farms, there is very little information about how these affect mortality of wild salmon, and this topic needs more research. Predation is probably the most important source of mortality, though diseased fish likely get eaten before they perish. A comprehensive review by Anthony (1994) discussed predatory birds, fish, and mammals as sources of marine mortality in salmon. The main mortality is believed to take place at the post-smolt stage, the first months after the smolts leave their home rivers. This is based on the assumptions that small fish are exposed to a larger range of predator species than large fish and that there are more predators inside the continental shelf than in oceanic areas.

Predation on smolts and post-smolts may be most severe in estuaries and fjords, just after the smolts have left freshwater. In the estuaries of the River Surna and River Orkla, Norway, heavy predation by fish, mainly cod, has been observed on both hatchery-reared and wild smolts (Hvidsten and Møkkelgjerd 1987; Hvidsten and Lund 1988). Higher survival of hatchery-reared smolts was obtained when they were transported by well-boat and released in the ocean outside the River Surna (Gunnerød et al. 1988), but straying of the returning adults increased considerably. This is consistent with the results reported by Solazzi et al. (1991) for coho salmon. In another Norwegian estuary, Reitan et al. (1987) showed that many migrating smolts were eaten by sea birds. Smolts released from hatcheries may experience relatively greater predation rates due to the effects of osmotic stress (Järvi 1989) and may also suffer high rates of predation owing to their lack of prior exposure to predators (Järvi and Uglem 1993).

The timing of smolt migration may be critical for survival. Several pieces of information strongly suggest the existence of a survival window which is open for a few weeks during spring and gradually closes during the summer (Larsson 1977; Hansen and Jonsson 1989). This effect is likely to be driven in part by endogenous factors related to smolt transformation, but it may be also be affected by extrinsic factors in the river, estuary, or at sea. In Norwegian rivers draining areas with high snow fall, the current velocity and turbidity increase considerably during snow melt. Hatchery-reared smolts in the Gaula and Surna rivers showed higher survival when they were released at high water discharge within the normal period of migration (Hvidsten and Hansen 1988), consistent with results in Maine (Hosmer et al. 1979). Survival may have been improved because the smolts move close to the water surface (Holm et al. 1982) and descend more quickly at high current velocity (Youngson et al. 1989), and they may be less vulnerable to predation owing to the high turbidity.

Survival of post-smolts may also be connected with abundance of suitable prey, particularly during the period immediately after they leave freshwater. When the smolts enter saltwater their expenditure of energy increases (Farmer et al. 1978) and scarce food resources may result in increased mortality. Lack of food would also reduce growth rate and increase their vulnerability to size-selective predation. Data on predation in the ocean are scarce but it has been speculated that sharks and skates may eat salmon, and there is some documentation of consumption by seals and whales (Pierce et al. 1991; Shearer 1992; Hislop and Shelton 1993).

The decreased Atlantic salmon abundance in recent years has been most pronounced in North America, although there is also a significant decrease in Europe, particularly in the southern areas (ICES 1996). There are several factors causing this decline, including freshwater habitat degradation, pollution, parasites such as *Gyrodactylus salaris*, and overexploitation. However, the decline is more pronounced for MSW salmon than for grilse, suggesting that changes in the marine environment may affect the survival of salmon in the sea (e.g., Ritter 1989). Friedland et al. (1993) showed that interannual variation in the area of potential post-smolt

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habitat at sea, defined as the area combining their optimal temperature and full marine salinity, is significantly correlated with catches of salmon from this area. Further studies, using time series of smolt survival rates, seem to confirm this.

If the driving force behind marine mortality is temperature related, one might predict that survival of salmon stocks migrating as post-smolts into the same area would be correlated. This hypothesis was tested using time series of survival estimates of wild salmon from the River Figgjo, Norway, and the North Esk, Scotland (Friedland et al. 1998). These rivers enter at opposite sides of the North Sea at about the same latitude and salmon from both rivers have been observed in the Faroes fisheries at the same time: Hence it was assumed that both groups are subjected to the same marine environment for at least the first months at sea (both stocks migrate to sea in early May). Return rates of 1 and 2SW salmon from Figgjo were significantly correlated, as were 1 and 2SW salmon from the North Esk, supporting the hypothesis that most mortality takes place in the first year at sea. Furthermore, there were significant correlations in return rates between salmon from both rivers, suggesting that survival was driven by common marine factors. A positive correlation was found between the area of 8–10°C in the Norwegian Sea north of the outlet of the respective rivers in May and the survival of salmon, consistent with the hypothesis of temperature-related mortality in the sea.

Research on reared Pacific salmon has indicated that marine survival is positively correlated with smolt size among sockeye salmon populations (Koenings et al. 1993). Within populations, larger individuals are more likely to survive than smaller individuals migrating to sea in a given year (chum: Healey 1982*b*; sockeye: Henderson and Cass 1991; coho: Mathews and Ishida 1989; Holtby et al. 1990; cutthroat trout: Tipping and Blankenship 1993; steelhead: Ward and Slaney 1988; Ward et al. 1989). However, the relationship between size and marine survival is complicated by several factors. First, interannual variation in marine survival is not correlated with smolt size within wild sockeye (Henderson and Cass 1991) or coho salmon populations (Holtby et al. 1990) but seems to be controlled by climatic factors (see below). Second, studies which have systematically controlled smolt size and date of release from hatcheries have revealed that survival is more strongly related to the date of seawater entry than body size (e.g., coho: Bilton et al. 1982; Morley et al. 1988). Finally, migration date of wild smolts is often related to fish size or age (larger and older smolts leave first; e.g., coho salmon: Irvine and Ward 1989; sockeye salmon: Crawford and Cross 1992), further complicating interpretation of data on survival.

The 1983, the El Niño – Southern Oscillation event in the northeast Pacific Ocean reminded many of the region's fisheries scientists of the importance of interannual variation in oceanographic conditions for fish (Wooster and Fluharty 1985; Mysak 1986). Both growth and survival at sea vary considerably from year to year and have been correlated with oceanographic conditions (e.g., Fraser River sockeye salmon: Hsieh et al. 1991). Research on sockeye salmon from Chignik Lake, Alaska, showed a positive correlation between growth at sea, inferred from scale measurements, and winter sea-surface temperature from 1952 to 1992 (Bumgarner 1993). Moreover, the abundance of adult Chignik Lake sockeye was positively correlated with both growth at sea and winter sea-surface temperature.

Despite the obvious importance of ocean conditions, salmon survival patterns are not consistent among regions. Variability in stock-recruitment relationships of Bristol Bay sockeye salmon was strongly correlated with climatic factors but correlations between climate and Fraser River sockeye productivity were weak (Adkison et al. 1996). The 1983 El Niño event was associated with poor survival and growth of coho and chinook salmon populations that feed off the Oregon coast but populations feeding farther north showed no effect (Johnson 1988). Coastal upwelling seems to exert a positive effect on Oregon coho salmon survival, though the evidence is not always strong and the mechanisms are unclear (Scarnecchia 1981; Holtby et al. 1990; reviewed by Pearcy 1992). Nickelson (1986) found that the marine survival of Oregon coho salmon was density independent and was influenced by upwelling, and Holtby et al. (1990) reported significant correlations of salinity with early marine growth and survival of coho salmon from coastal British Columbia. Fisher and Pearcy (1988) concluded that upwelling was positively correlated with survival of Oregon coho salmon but that growth was good over a range of upwelling conditions.

While the direct links to salmon are unclear, there is convincing evidence that the last century has seen long-term climate changes affecting freshwater and marine ecosystems in the north Pacific Ocean (Mantua et al. 1997) with incident changes in zooplankton (Brodeur and Ware 1992; Brodeur et al. 1996) and salmon production (Rogers 1987*b*; Pearcy 1992; Beamish and Bouillon 1993; Beamish 1994; Hare and Francis 1995; Francis and Mantua 1998). In general, when conditions are favorable for survival in northern regions (e.g., Alaska), they may be unfavorable in southern regions (Francis and Sibley 1991), but it is not clear how general this anti-correlation is, or where the geographical "breakpoint" might be.

Oceanic homing migration

Atlantic salmon leave the ocean feeding grounds after 1–4 yr. The factors initiating the homeward migration are unknown but salmon have circannual rhythms of reproductive hormones, synchronized by photoperiod (Bromage et al. 1993). The usual pattern is that the older individuals return earlier in the season than younger ones (e.g., Dunkley 1986; Jonsson et al. 1990; Shearer 1992). The internal rhythms and responses to photoperiod are probably population specific, however. For example, salmon ascend several Scottish rivers during all months of the year (e.g., Mills 1989) whereas in Norway salmon ascend rivers only from May to October. There is direct evidence for a genetic component in the seasonal return migration of Atlantic salmon (Hansen and Jonsson 1991), as in Pacific salmon (Ricker 1972; Taylor 1980; Gharrett and Smoker 1993).

From extensive data on tagged salmon, Hansen et al. (1993*b*) concluded that the homing migration from the feeding areas in the north Norwegian Sea to natal rivers in Norway consists of two phases: an initial phase with orientation from the feeding areas towards the Norwegian coast and a

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second phase in coastal and estuarine waters with more precise orientation towards the home river. Hansen et al. (1993*b*) estimated that salmon traveled 50–100 $km d^{-1}$ in the Norwegian coastal current. The rather rapid travel rate of Atlantic salmon in the open ocean is consistent with data from the Pacific salmon species migrating in the open ocean, where maturing salmon may average 40–60 $km d^{-1}$ and occasionally more than 80 $km d^{-1}$ over long distances (Royce et al. 1968; French et al. 1976; Groot and Quinn 1987).

Little is known about the mechanisms of homing by Atlantic or Pacific salmon on the open ocean. Some models for salmon in the north Pacific (e.g., Saila and Shappy 1963; Jamon 1990) have indicated that very little orientation is needed to simulate the return rates of tagged fish from the ocean to coastal areas but these models are inconsistent with empirical data of various sorts, invalidating their conclusions (Quinn and Groot 1984; Quinn 1991). If we reject the hypothesis of random movement, three alternatives present themselves: navigation, orientation, and piloting (Griffin 1952). Navigation is the ability to select and maintain directional movement towards a goal without reference to stimuli emanating from the goal and seems to necessitate some form of map to indicate the individual's location, relative to the goal. There is no direct evidence that salmon navigate but the tendency of at least some populations to converge on specific coastal locations from very broad feeding ranges suggests such an ability (Quinn 1984, 1990). Behavioral experiments with juvenile salmon indicate that they are sensitive to the magnetic field of the earth (Quinn 1980; Quinn and Brannon 1982) and magnetite particles may be a component of the transduction mechanisms (Walker et al. 1988; Moore et al. 1990; Walker et al. 1997). Such a magnetic field detection system could aid in salmon navigation but no conclusive field experiments have been conducted on this subject.

Alternatively, the salmon may possess a compass orientation ability and head in a homeward direction without regard to their location at sea. This hypothesis is consistent with interannual variation in timing and landfall of Fraser River sockeye salmon (Blackbourn 1987*b*; Groot and Quinn 1987) and with experimental evidence that juvenile salmon can orient using the sun's position (Groot 1965) and magnetic field (Quinn 1980; Quinn and Brannon 1982). The ability of telemetered Atlantic and Pacific salmon to swim in relatively straight lines in open water indicates at least some directional ability (Smith et al. 1980; Quinn et al. 1989; Ogura and Ishida 1995) and rapid rates of net travel could not be accomplished without a good sense of direction, given the swimming speeds of salmon (Quinn and Groot 1984).

The interannual variation in migration timing provides some information on the orientation mechanisms of salmon populations. Burgner (1980) reported that sockeye salmon return early to Bristol Bay, Alaska, following a relatively warm spring. This relationship is not species specific however; the run of sockeye salmon to the Fraser River, B.C. tends to be late following a relatively warm spring (Blackbourn 1987*b*; Quinn 1990). Blackbourn (1987*b*) hypothesized that the ocean distribution of sockeye salmon shifts to the north or south, depending on prevailing water temperatures, and the date of migration is fixed. Thus after a warm spring, populations in the northern part of the range (e.g., Bristol Bay) have a shorter migration and arrive sooner whereas southern populations such as the Fraser River tend to arrive late because they have farther to go. The migratory routes of salmon also reflect oceanic conditions. The proportion of sockeye salmon migrating to the Fraser River via Johnstone Strait (i.e., northern route, as opposed to the southern route through the Strait of Juan de Fuca) is positively correlated with water temperatures (Groot and Quinn 1987; Xie and Hsieh 1989). Computer simulations indicated that ocean currents can also affect latitude of landfall (Thompson et al. 1992) and timing of return (Thompson et al. 1994).

In addition to the map and compass hypotheses, it is possible that salmon migration at sea is accomplished by piloting, using information learned on the outward journey or clues emanating from freshwater locations. However, the distances that salmon travel from their home river, the complex current patterns at sea, and the tendency of salmon to return home from different feeding locations makes it very unlikely that riverine odors play an important role on the open ocean (Royce et al. 1968), and it is generally accepted that the stimuli guiding salmon at sea differ from those used in rivers (Hasler 1971; Quinn 1990). In addition, some populations (e.g., Fraser River sockeye salmon) do not return as adults along the route that they took as smolts, so information learned on the outward journey cannot be crucial for homing (Groot and Cooke 1987).

After salmon accomplish the migration from distant, oceanic feeding grounds to the nearshore environment, the coastal waters and estuaries present another set of challenges to their orientation systems. The homing migration of Atlantic salmon does not seem to be passive or current guided, as suggested by Taguchi (1957), Mathisen and Gudjonsson (1978), and Isaksson (1980). When homing to Norwegian rivers the fish approached the fjords from both the north and south and may have followed the coastline for long distances (Hansen et al. 1993*b*). A similar pattern has also been observed along the east coast of Canada (Reddin and Lear 1990). Salmon tracked by Smith et al. (1980) off the east coast of Scotland showed the ability to swim in fixed directions at energetically efficient speeds but were also affected by tidal currents (see also Quinn 1988 for similar results with sockeye salmon).

Hansen et al. (1993*b*) reported that Atlantic salmon travel rates slowed in fjords, perhaps because they require time to locate their natal rivers. Westerberg et al. (1982*a*) and Døving et al. (1985) reported that telemetered salmon moved up and down in the water column in association with fine-scale hydrographic stratification and they concluded that salmon search for vertical gradients of odors from the home river rather than horizontal gradients. The role of such vertical movements in orientation is consistent with observations of sockeye salmon (Quinn et al. 1989) but modeling suggested that the sockeye used a combination of compass orientation, avoidance of freshwater from nonhome sources, and random movement when they encounter islands and other obstacles (Pascual and Quinn 1991).

Alternatively, the slow and sometimes apparently random movements of many salmon in coastal waters and estuaries may not reflect orientation mechanisms but the tendency of many populations to wait for suitable conditions for up-

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stream migration (Jonsson et al. 1990) or to remain in the estuary as they undergo the physiological processes of maturation and osmoregulatory adaptation to freshwater. Atlantic salmon tracked in estuaries of the Baltic Sea (Westerberg 1982*b*), Nova Scotia (Brawn 1982), and England (Potter1988; Priede et al. 1988) tended to move back and forth with tidal currents for some time before ascending their home river. This, too, is consistent with the behavior of many populations of Pacific salmon (e.g., Groot et al. 1975; Olson and Quinn 1993; Levy and Cadenhead 1995).

Although olfaction probably plays little role in the orientation of salmon on the open ocean, it is well established that odors guide the final stages of homing in freshwater. A large body of evidence indicates that odors inherent in the stream (e.g., rocks, soil, plants) provide a distinctive chemical signature that is learned (imprinted) by juvenile salmon prior to or during seaward migration and is used by maturing adults to identify their natal stream. (Hasler 1966; Harden Jones 1968 Hasler and Scholz 1983; Hansen et al. 1989; Dittman and Quinn 1996). It has also been hypothesized that population-specific odors (pheromones) from conspecifics living in the river or migrating to sea guide maturing salmon (Nordeng 1977, 1989). Most evidence supports the first hypothesis. Atlantic salmon released as smolts in a small stream devoid of salmon returned there to spawn at maturity (Hansen et al. 1989). Pacific salmon also returned to their release site rather than to a site containing members of their population (e.g., Donaldson and Allen 1957; Brannon and Quinn 1990) and can home to rivers scented with artificial odors on which they imprinted, even in the absence of pheromones (Hasler and Scholz 1983).

Experimental transportation and release studies indicate that salmon may not merely imprint once in freshwater but rather that odors are learned in a more complex sequence. Atlantic salmon released as smolts in the River Imsa returned there as adults with high precision (Hansen et al. 1989). However, when smolts imprinted to River Imsa water were transported by boat about 45 km towards the ocean, and thus deprived of a part of the migration route, the great majority of the adults failed to return to River Imsa, suggesting that the salmon needed to experience the outward migration in order to find their home river at maturity. Atlantic salmon transported and released as post-smolts on the feeding grounds north of the Faroe Islands failed to home as adults to their home river; in fact, no fish was reported caught in fresh water (Hansen et al. 1993*b*). This may indicate a reduced preference for these fish to enter rivers and spawn. All adult recaptures, however, were made in Norwegian home waters eastward of the site of release. No maturing salmon were reported from elsewhere despite heavy salmon fishing in the U.K., Ireland, and North America, and in Icelandic rivers. Natural mortality of post-smolts in the sea is high (e.g., Mills 1989) and the recaptures are few and scattered over large areas. However, the fact that all adult recaptures were reported from Norwegian home waters supports the idea that the salmon may have an inherited crude compass sense of direction (Walker et al. 1988; Moore et al. 1990) and that sequential learning may not be mandatory to sense the general direction back to Norway. The iteroparous life cycle of Atlantic salmon provides an opportunity for further insights in the imprinting process because there is the possibility that they might imprint as seaward-migrating post-spawners. However, Hansen and Jonsson (1994) provided evidence to support the hypothesis that the learning process during migration to the sea as smolts becomes fixed and is not overridden by a new learning process at the post-spawning stage. Kelts transplanted from their home river to several distant rivers returned as second-time spawners to the river they left as smolts, not to the river from which they entered the ocean as adults.

Summary

The marine phase of the Atlantic salmon's life cycle is much less understood than the freshwater phase. Information on general distribution patterns in time and space for major stock complexes has been assembled but is biased by reliance on uneven fishing effort for recoveries of marked fish and hampered by rather small sample sizes in many cases. The sources of mortality are virtually unknown but evidence points to the first few months at sea as being critical for survival and correlations with oceangraphic conditions are providing some insights, albeit indirect, into the processes operating at sea. The trophic ecology of salmon at sea is in a similarly primitive state of understanding. Information from stomach contents has yet to be integrated into a model of prey resources and energetics that would shed light on factors that might limit growth and affect age-at-maturity and survival. In these and other aspects of the biology of Atlantic salmon at sea such as migratory orientation, many insights are provided by research on the more abundant and heavily studied Pacific salmon species. Atlantic salmon seem to be most comparable to stream-type chinook salmon or steelhead in their size at seawater entry, migratory patterns, trophic status, and overall abundance. Information on these species in particular, and other Pacific salmon as well, may be useful in understanding Atlantic salmon biology and we encourage further comparative analyses that may advance the state of knowledge on salmonids in both oceans.

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Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events

Kevin D. Friedland

Abstract: Ocean climate and ocean-linked terrestrial climate affect nearly all phases of Atlantic salmon (*Salmo salar*) life history. Natural mortality in salmon occurs in two main phases: juvenile stages experience high mortality during freshwater residency and pre-adult salmon experience high mortality in estuarine and ocean environments. Freshwater survivorship is well characterized and tends to be less variable than marine mortality. Sources of marine mortality are poorly known due to a lack of basic knowledge about post-smolt distributions and habits. Coherence patterns among regional and continental stock groups suggest broad scale forcing functions play a more important role in defining recruitment than mortality effects associated with individual rivers. The action of mesoscale regional environment is most prominent during the post-smolt year when survival, maturation, and migration trajectories are being defined. During the early weeks at sea, growth mediated survival defines recruitment patterns. A correlation between sea surface water temperature and survival has been observed for salmon stocks in the northeast Atlantic suggesting temperature either directly affects growth or modifies post-smolt behavior. Age at first maturity is controlled by environmental as well as genetic factors. The abundance of two seawinter spawners in North America is directly scaled to the size of overwintering thermal habitat in the northwest Atlantic, which suggests a link between maturation and environment.

Résumé : Le climat océanique et le climat terrestre lié à l'océan influent sur presque toutes les phases du cycle vital du saumon de l'Atlantique (*Salmo salar*). La mortalité naturelle du saumon se produit dans deux phases principales : les juvéniles connaissent une forte mortalité durant leur séjour en eau douce, et les pré-adultes meurent en grand nombre dans les milieux estuariens et océaniques. La survie en eau douce est bien caractérisée et tend à être moins variable que la mortalité dans le milieu marin. Les causes de mortalité dans le milieu marin sont mal connues en raison de notre manque de connaissances de base concernant les répartitions et les moeurs des post-smolts. Les profils de cohérence entre les groupes de stocks régionaux et continentaux laissent penser que des phénomènes de forçage à grande échelle jouent un rôle plus important dans la détermination du recrutement que les facteurs de mortalité liés aux rivières prises individuellement. L'action du milieu régional à échelle moyenne est maximale durant l'année de post-smolt où la survie, la maturation et les trajectoires migratoires sont définies. Durant les premières semaines en mer, la survie liée à la croissance définit les profils de recrutement. On a observé une corrélation entre la température de l'eau de la surface de la mer et la survie chez les stocks de saumon du nord-est de l'Atlantique, ce qui laisse penser que la température affecte directement la croissance ou modifie le comportement des post-smolts. L'âge à la première maturité est déterminé par des facteurs tant environnementaux que génétiques. L'abondance des géniteurs dibermarins en Amérique du Nord est directement proportionnelle à la taille de l'habitat thermique hivernal dans le nord-ouest de l'Atlantique, ce qui laisse penser qu'il existe un lien entre la maturation et l'environnement.

[Traduit par la Rédaction]

Introduction

Survivorship in Atlantic salmon (*Salmo salar*) populations can be partitioned by mortality occurring in freshwater and mortality occurring during the marine phase. Mortality rates during the freshwater phase are estimated with a great deal of accuracy and precision because freshwater populations are accessible. Freshwater populations can be censused by fences or barriers that allow exact counts of migrating adults and juveniles. Marine mortality has been more difficult to assess. After salmon smolts migrate to sea they are usually uncensused until they appear in fisheries over a year later. For decades the life history of post-smolts was virtually unknown. Only recently have survey designs improved to allow characterization of post-smolt distribution, diet, and survivorship (Shelton 1997). These new surveys, in combination with indirect methods that make use of a variety of existing data, have allowed scientists to make new inferences about salmon in the sea.

One of the simplest and most effective uses of existing datasets has been to examine coherence patterns in abundance and catch time series data. Coherence, or synchrony, refers to the common response of fish stocks to environmental effects over broad spatial scales. Coherence has been observed in groundfish and pelagic species (Koslow et al. 1987; Zebdi and Collie 1995); however, the caveat that applies to other species, as well as salmon, is that the appropriate spatial scale of coherence is often difficult to estimate (Cohen et al. 1991; Myers et al. 1995). In Atlantic salmon, the strong stock and recruitment relationships that exists between egg deposition and juvenile production (Symons 1979; Chadwick 1982; Buck and Hay 1984) are often

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K.D. Friedland. UMASS/NOAA CMER Program, Blaisdell House, University of Massachusetts, Amherst, MA 01003, U.S.A. e-mail: friedlandk@forwild.umass.edu

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difficult to match in the eventual relationships that emerge between egg deposition and adult recruitment (Solomon 1985; Elliott 1993). Sea survival is generally more variable than freshwater survival (Chadwick 1987) and the emerging paradigm is that covariation among stocks is driven by broadscale climate fluctuations (Adkison et al. 1996). The action of mesoscale regional environment is most prominent during the post-smolt year when survival, maturation, and migration trajectories are being defined. However, the action of ocean driven environment on freshwater production and smolt migration play important roles as well.

Recruitment in Atlantic salmon populations is controlled by events that take place during their first year at sea (Scarnecchia et al. 1989; Salminen et al. 1995; Friedland et al. 1998*a*). Variation in recruitment translates directly into catches in commercial and recreational fisheries and spawning escapement. Thus, post-smolt mortality and the factors that control its annual variation are of paramount interest to scientists and managers. Furthermore, the highest marine natural mortality rates in salmonids are believed to occur during the first weeks to months at sea (Fisher and Pearcy 1988; Holtby et al. 1990; Eriksson 1994; Salminen et al. 1995). These mortality effects are believed to be growth mediated during this period due to either variation in ocean productivity, interspecific competition, or intraspecific interactions (Ricker 1962; Neilson and Geen 1986; L'Abee-Lund et al. 1993; Friedland et al. 1996). Therefore, broad scale processes that affect salmon growth are of great interest. However, in addition to mortality effects, annual variation in the rate of sexual maturity also influences recruitment patterns to fisheries and escapement at various ages. Both stock genetics and environmental effects pattern sexual maturation; the relative influences of these effects on maturation, especially as it relates to maturation after only a single year at sea, is still being actively researched (Thorpe 1994; Friedland and Haas 1996; Friedland et al. 1996). However, it is clear that stocks have different maturity schedules, often associated with latitude, and that age-at-maturity can change over time (Power 1981; Saunders 1981; Shearer 1990; Summers 1995).

Mortality and maturation mechanisms in salmon appear to be linked to ocean climate. Maturation, as evidenced by returns and survival of various aged salmon, has been shown to vary in correlation to a number of environmental signals such as temperature (Saunders et al. 1983; Scarnecchia 1983; Martin and Mitchell 1985; Scarnecchia et al. 1991; Friedland et al. 1993). However, in some cases ocean conditions associated with growth and maturation co-vary with conditions affecting the survival of smolts entering the sea (Scarnecchia et al. 1989). Survival of Pacific salmon species have been shown to vary with fluctuations in broadscale circulation patterns like ENSO events (Johnson 1988; Beamish and Bouillon 1993; Francis and Hare 1994) and more localized upwelling circulation that would be expected to impact local productivity and juvenile salmon growth (Fisher and Pearcy 1988; Kope and Botsford 1990). Even in confined systems like the Baltic Sea, the effects of temperature and circulation have been identified as determinants of growth and survival (Salminen et al. 1995).

In this paper, I will examine the general question of how climate impacts critical Atlantic salmon life history processes across freshwater and marine habitats, especially focusing on mortality and maturation. I will first review coherence patterns in regional stock groups of Atlantic salmon and consider what they suggest about the relative role of freshwater and marine mortality effects. I will then consider the effect of ocean-linked climate patterns on freshwater recruitment and growth and examine climate linkages to migration cues. Next, I will describe relationships between early post-smolt survival and ocean climate observed for Atlantic salmon populations in the northeast Atlantic. Finally, I will try to relate environmentally guided migration trajectories to the maturation process.

Coherent trends in regional population groups

Scale for coherence patterns

Coherence patterns in Atlantic salmon have been observed on continental and regional scales. Friedland et al. (1993) observed significant correlation among survival time series for five salmon stocks ranging geographically from Newfoundland to the northeast United States, which represents nearly the entire range of Atlantic salmon in North America. Coherence patterns can also be specific for sea age of return. Return rates for two sea-winter (2SW) salmon in the Penobscot and Saint John rivers in North America are highly correlated despite differences in the return rates for 1SW fish which comprise approximately 10% of the Penobscot stock and 60% of the Saint John runs (Friedland 1994). Correlation for groups of Icelandic rivers was demonstrated by examining catch time series (Scarnecchia et al. 1991). Grilse catch time series formed two clusters, one comprised of northeast coast rivers, the other northwest coast rivers. A stock clustering in central Europe is also evident from return rate data for wild stocks from southern Norway and western Scotland (Friedland et al. 1998*a*). Grilse return rates for the Figgjo and North Esk rivers, both of which empty into the North Sea, are highly correlated, whereas, the 2SW rates for the same rivers are less well correlated (Fig. 1). Population data for stocks outside the North Sea area suggest that survivorship varies regionally for other European stocks (Crozier and Kennedy 1993). Finally, correlation among catch time series for continental stock complexes suggests teleconnections may exist between the eastern and western North Atlantic. Fisheries have been largely unrestricted in North America and Europe for the period 1960–1995 with the exception of management measures implemented in recent years. The contrast in catch trends is large and can only be explained by changes in natural mortality and the recruitment process. The change in exploitation necessary to produce the observed change in catch is unrealistic and inconsistent with exploitation patterns observed from tagging experiments. Significant correlation between North American and southern European catches suggests a linkage between both complexes and a common environmental signal (Fig. 2C). However, this linkage is not as well developed between the northern European complex and either southern Europe or North American complexes, suggesting these stocks utilize different rearing areas and migrational pathways (Figs. 2A, 2B). Greenland and Faroese catches reflect the stocks harvested in the respective fishing zones

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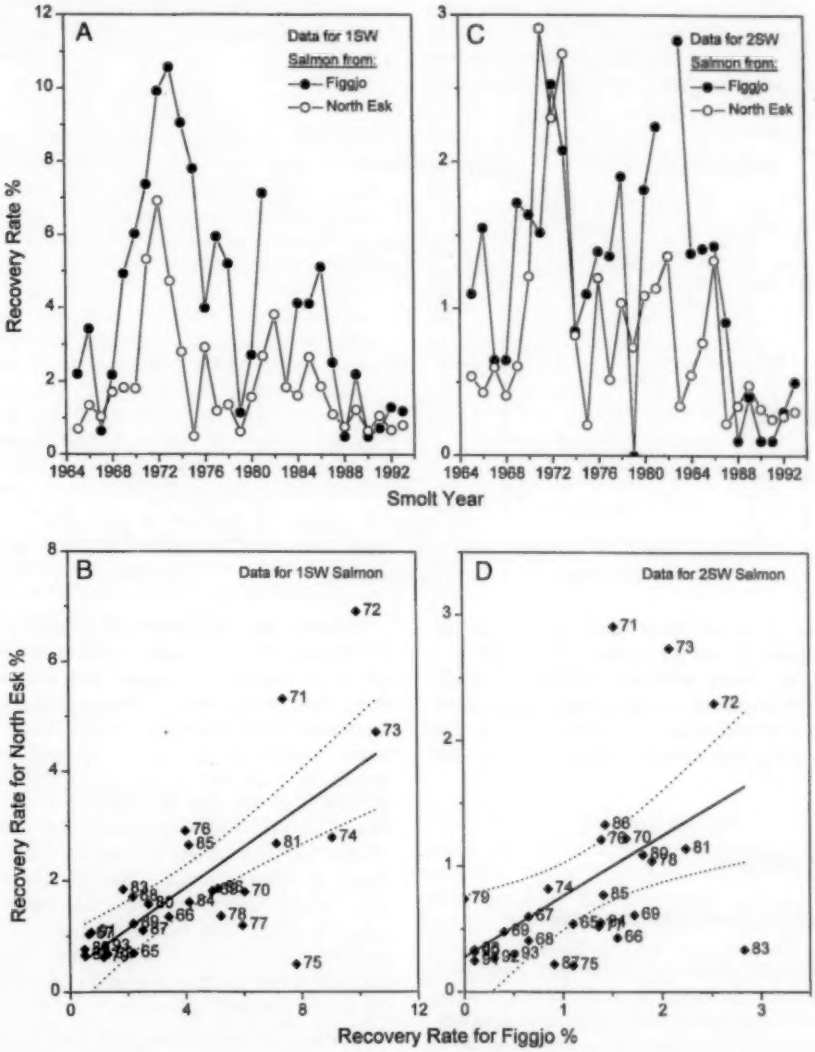
Fig. 1. Tag recovery rate for 1SW salmon to the rivers Figgjo and North Esk versus year (A); tag recovery rate for 1SW salmon to the river Figgjo versus recovery rate for the North Esk (B); tag recovery rate for 2SW salmon to the rivers Figgjo and North Esk versus year (C); tag recovery rate for 2SW salmon to the river Figgjo versus recovery rate for the North Esk (D). Smolt year labels points on the scattergrams (from Friedland et al. 1998*a*).



(Figs. 2D, 2E, 2F). From these analyses, it appears coherence is operating on continental and regional scales in Atlantic salmon. Despite the length of ocean migrations for the species, neighboring stocks appear to respond similarly to ocean conditions; thus we see many examples of allied river stocks with similar survival patterns. The scaling of these phenomena to the continental level suggests broadscale climate patterns, which simultaneously affect all regions of the ocean, are also at work.

Spatial relationship and location for coherence

A common pattern of catches and marine survival for any grouping of Atlantic salmon stocks suggests that factors controlling annual survivorship act nearly equally on all stocks in the group. This challenges conventional concerns about the natural mortality that occurs in river, estuary, or near-shore marine ecosystems proximate to natal rivers (Larsson 1985; Wood 1987; Hvidsten and Lund 1988; Magnhagen 1988). It is unlikely that riverine mortality could be synchronously linked with riverine mortality for fish emigrating from a river located in another geographic area. The correlation between survival rates suggests an important source of mortality acts on the stocks when they are in a common place or being acted upon by a common set of conditions. Since they are migrating from distinct locations, the longer they are at liberty, the greater the likelihood their distributions will begin to overlap. Under this scenario, more localized impacts may affect stocks if they share a common

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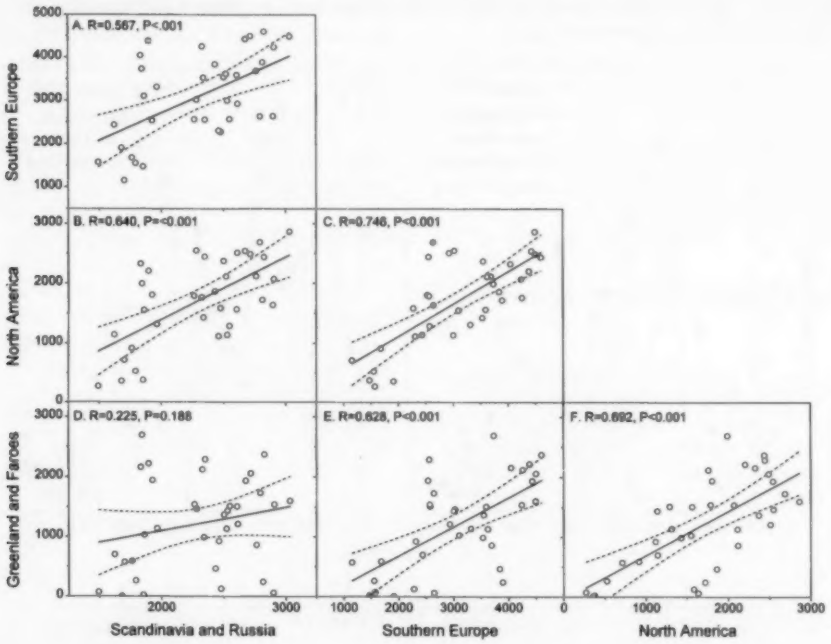
Fig. 2. Scattergram matrix of total reported catch time series, 1960–1995, for regional groups of the North Atlantic area. All catches are in metric tonnes.



migration destination. If on the other hand, the critical period for survival is early in the post-smolt year, there is a greater chance that the stocks will not be homogeneously mixed during the critical period. If coherence exists under these circumstances, it would argue for survival effects that act on broad spatial scales thus affecting stocks that may not overlap spatially.

Land–sea interactions

Ocean-driven effects on freshwater production of juveniles

Climate affects Atlantic salmon in freshwater through a number of physiological, behavioral, and feeding-related mechanisms. The main parameter defining spatial relationships and habitat suitability in freshwater is in-stream flow. In-stream flow, which is mediated by rainfall amounts, shapes spawning and juvenile habitats by mechanical means (Waters 1993). Production is further defined by the feeding opportunities and growth conditions associated with various habitats, again flow being a primary determinant (Gibson and Myers 1988; Mills 1989; Kennedy and Crozier 1993). Seasonal variations in mortality can be significant and are related to climate-mediated stress factors (Cunjak and Randall 1993). The migration from freshwater may be a source of significant mortality that can be ameliorated by river flows (Hvidsten and Hansen 1988). To the extent climate variation, both short-term variation and trend, are mediated by the same ocean-linked mechanisms affecting salmon during the marine phase, freshwater and marine productivity may also be linked.

Juvenile salmon growth and habitat is largely determined by climate effects related to prevailing temperature regimes and flow conditions. Regier and Meisner (1990) outlined three main areas where climate change is likely to impact freshwater fish populations: temperature, water quantity, and water quality. Regional or seasonal temperature change would be expected to directly influence juvenile salmon growth and the age at which fish smoltify and mature. Minns et al. (1995) simulated the effect of temperature change on populations in eastern Canada by calibrating a model of smolt age that is based upon temperature and latitude. Model results suggested that smolt age would significantly decrease with increasing temperature. Mangel (1994) derived similar model results, but further illustrated the reach of ocean climate change by also showing the expected change in maturity schedules.

Increases in temperature also pose a direct threat to populations at the southern end of the species' range. Some populations experience near lethal thermal conditions during summer making any further increase in temperature intolerable (Power 1990). Changes in rainfall patterns, especially as they relate to diminished flows in streams and rivers, may severely impact productivity of salmon populations. Minns et al. (1995) examined the effect of anticipated changes in flow on the concomitant change in the amount of suitable rearing habitat for Atlantic salmon in eastern Canada. These changes suggest that the production potential of regional salmon stocks could be severely limited.

Water quality encompasses a wide spectrum of effects from physical attributes of a system to its biological productivity. Climate change may shift nutrient loading patterns, cause oxygen stress, or actually shift the composition of the

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forage base for juvenile fish (Henderson et al. 1992). Modeling by historical analogy offers useful predictive tools to deal with anticipated climate changes (Neitzel et al. 1991). Additionally, it has been shown that river flows can be used effectively in models of combined marine–freshwater effects on salmon production (Scarnecchia 1981; Scarnecchia et al. 1989).

Migration timing

Among the many traits locally adapted in individual salmon stocks, cued migration behaviors are some of the most important. The two main cues identified in the initiation of smolt migrations are climate-related factors. Water temperature has been identified by numerous authors as a key factor stimulating smolt migration (Solomon 1978; Jonsson and Ruud-Hansen 1985; Jonsson et al. 1989). Stream and river water temperatures reflect regional weather patterns and thus would be correlated to annual production cycles in the coastal ocean. Response to temperature cues would reliably synchronize migration to a particular production event (Friedland and Haas 1988). In some river systems, there is insufficient contrast in spring water temperatures to reliably initiate smolt migration, thus waterflow has evolved as the primary cue (Österdahl 1969; Hestagen and Garnås 1986). Smolts entering the ocean either too early or too late would begin their post-smolt year on migrational trajectories that could be less than optimal in respect to feeding opportunities, invading predator fields, or thermal stress. Therefore, the evolution of these proximate migration mechanisms is critical.

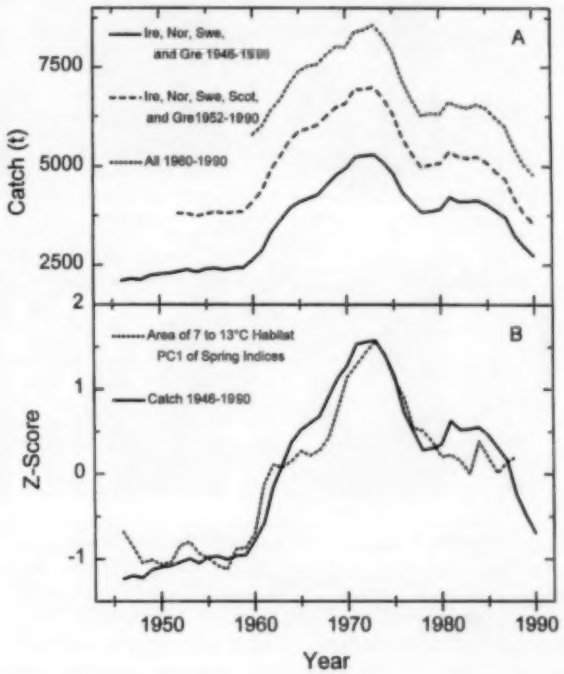
Ocean survival effects

Temperature distributions

The relationship between post-smolt survival of European salmon stocks and sea surface temperature distribution was first noticed by Friedland et al. (1993). A composite catch time series was used as a surrogate for post-smolt survival and population abundance. Most of the catch in the time series is from grilse catches; therefore, it is assumed that annual variation in maturation does not play a large role (Fig. 3A). Spring thermal habitat was highly correlated with population abundance, suggesting that warmer conditions in spring favored post-smolt survival in the northeast Atlantic area (Fig. 3B). However, regional survival signals were mixed together to form this composite representation of European stocks. Also, thermal habitat was represented by the first principal component of monthly data, which tells us little about the temporal and spatial scale of sea surface temperature conditions important to the fish. As a consequence, it has been difficult to develop biological hypotheses to explain this correlation.

Friedland et al. (1998*a*) addressed these problems by narrowing the geographic scope of the stock groupings used in the analysis and by partitioning the thermal habitat calculations and correlations in time and space. In their study, the survival of only two index stocks, the Figgjo from southern Norway and the North Esk from Scotland (Fig. 1), were compared to thermal habitat time series partitioned by temperature, longitude, and month. Two important correlations

Fig. 3. Total nominal landing for the European stock complex (A) over three time periods: for 1946–1990 the catch of Ireland, Norway, Greenland (European component), Faroe Islands, and Sweden (west coast); for 1952–1990 the catch of Scotland is added to the time series; and for 1960–1990 all nations are included. Total nominal landing for the European stock is compared to the first principal component of spring habitat (B). Data are smoothed (from Friedland et al. 1993).



emerged from this analysis. The survivals of Figgjo and North Esk 1SW fish were negatively correlated with the area of 5–7°C SST in May (Figs. 4A, 4E). These correlations are strongest using data from centering longitudes in the range 0–4°E. The second correlation was a positive relationship between survival and the area of 8–10°C SST also in May (Figs. 4D, 4H). The peak correlations were achieved with data from centering longitudes more to the west than for the cold water correlations. The negative correlations observed for the 5–7°C habitat data are only more weakly echoed in the 6–8°C data (Figs. 4B, 4F) and no significant correlations appeared in the 7–9°C data (Figs. 4C, 4G).

These correlations are related to variation in sea surface temperature distribution in the North Sea and along the coast of Norway during spring. Spring warming during the period of high survival rates was more rapid than during the more recent period of lower survival. These differences can be most easily traced by following the area of 8–10°C water through the spring period, which is also biologically significant to juvenile salmon because it's the temperature at which post-smolts typically first enter the marine environment. In March during the 1970's period, 8–10°C SST was distributed west of Ireland and the United Kingdom and south of 63°N (Fig. 5A). This band of SST expanded north and eastward during April (Fig. 5B) and May (Fig. 5C) until the

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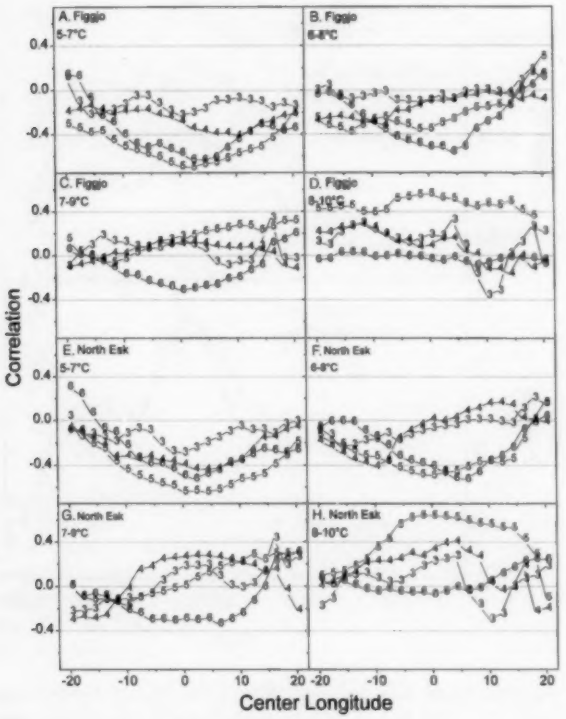
Fig. 4. Correlation between thermal habitat and recovery rate of 1SW salmon versus the center longitude used to calculate the thermal habitat time series. Each correlation is for data from a 22° longitude range. Data for the Figgjo stock and thermal habitat ranges of 5–7°C (A); 6–8°C (B); 7–9°C (C); 8–10°C (D). Data for the North Esk stock and thermal habitat ranges of 5–7°C (E); 6–8°C (F); 7–9°C (G); 8–10°C (H). Coordinates are labeled with numerical month of the year (from Friedland et al. 1998*a*).



North Sea and coastal waters off southern Norway were all in excess of 8°C. By early summer, 8–10°C water was distributed in the coastal waters off northern Norway and well into the Norwegian Sea (Fig. 5D). This is in contrast to the average distribution of SST during the 1980's period. March 8–10°C SST distribution was almost identical to the 1970's distribution (Fig. 5E); but, differences emerged by April when 8–10°C water extended much closer to the Norwegian coast than during the 1970's period (Fig. 5F). Likewise, in the May SST distributions, 8–10°C water did not reach the Norwegian coast and the northern North Sea remained cool (Fig. 5G). June distributions were generally similar to the 1970's period, except that the 8°C isotherm stayed below 70°N in the 1980's distribution (Fig. 5H).

Survival of salmon stocks from the North Sea area appear to be affected by the distribution of spring water temperatures in the northeast Atlantic. Survival fluctuated similarly for both 1SW and 2SW salmon for both index stocks, thus the contribution of maturation mechanisms to the observed return rates can be discounted. Survival for 1SW fish is recorded as the rate of return of tags versus the number released. The tagged fish were at liberty for the post-smolt year before being recovered, therefore, there is no way to know at what point the highest mortalities occurred during the post-smolt year. Eriksson (1994) reported the results of tagging experiments in the Baltic Sea in which post-smolt recoveries allowed for the estimation of weekly mortality rates for post-smolts. These rates were as high as 28% during the first two weeks at sea and declined rapidly thereafter. These results generally confirm the suspicions held by most salmon researchers that the highest mortality rates occur during this time period. The rates for the balance of the year are elevated as compared to those observed for adults, but they were nonetheless lower than the spring moralities. This draws our focus to the time period when Figgjo and North Esk salmon would first be entering the marine environment, which is also addressed by the sea surface temperature correlation analysis.

The strongest correlations between survival rate and areal extent of thermal habitat occurred during the month of May. In both stocks, correlation with warm water habitat (8–10°C) was restricted to May; whereas, correlations with cold water habitat were also observed for June data. The distribution of sea surface temperature, which in essence is driving these correlations, was found to be ecologically significant. Sea surface temperature distributions for periods of good versus poor salmon survival showed that when cool surface waters dominated the Norwegian coast and North Sea during May, salmon survival was poor. Conversely, when the 8°C isotherm extended northward along the Norwegian coast during May, survival was good. Thus, it is the variation in temperature conditions for this segment of the Norwegian coast that presents the greatest challenge to the post-smolts.

It is important to consider the transport mechanisms at work on salmon juveniles when they first go to sea. The area utilized by Figgjo and North Esk post-smolts is dominated by a coastal current that travels to the northeast at mean seasonal rates of approximately 13–17 km·d^{-1} (Hopkins 1991). Jonsson et al. (1993) reported that post-smolts in the same current had migratory speeds averaging 7.45 km·d^{-1} and that the fish were rarely able to transport themselves southward against the prevailing currents. Thus, salmon post-smolts from the Figgjo and North Esk would be expected to occupy the thermally dynamic segment of the North Sea and Norwegian coast found to vary in correlation to survival. How might variation in thermal conditions affect the survival of post-smolt salmon? The rejoinder to this question is that there are many ways, but two main groups of factors are growth-mediated effects and production mechanisms.

Growth-mediated effects

Temperature has a direct effect on growth that will affect growth-mediated sources of mortality in post-smolts. Survival is inversely related to body size in pelagic fishes (Peterson and Wroblewski 1984). Growth-mediated survival, and especially how it relates to the ecology of early life history stages, is broadly identified as critical to the recruitment process (Anderson 1988; Pepin 1991). This has been seen in salmonids where growth-related mechanisms have been associated with mortality rates (Furnell and Brett 1986; Mathews and Ishida 1989; Holtby et al. 1990; L'Abee-Lund et al. 1993; Friedland et al. 1996). Post-smolt growth increases in a linear trend with water temperature up to a

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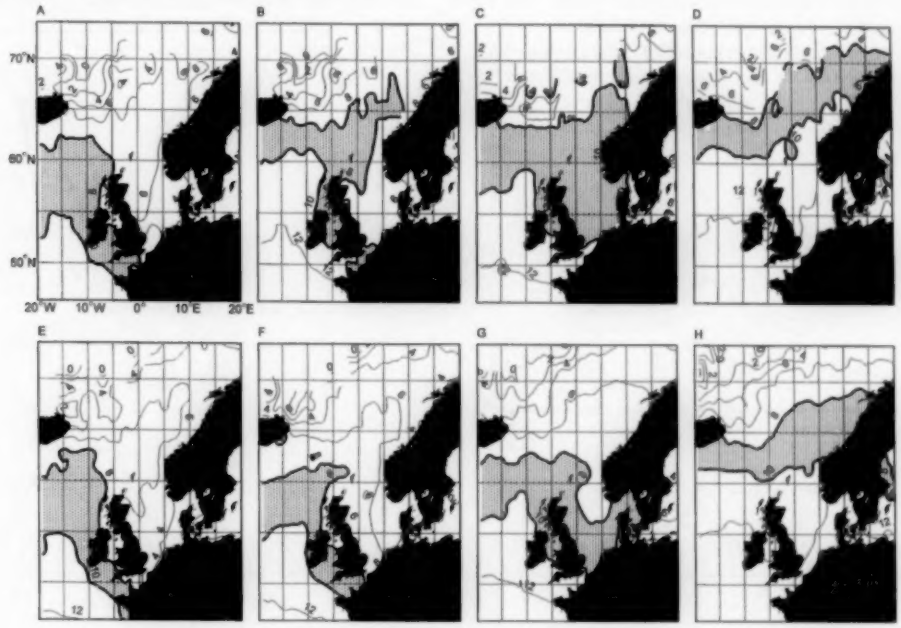
Fig. 5. Sea surface temperature maps of the Northeast Atlantic area with 2°C isotherms and the SST area of 8–10°C marked with hatching for the period 1971–1974, months March (A); April (B); May (C); June (D). Data for period 1985–1988, months March (E); April (F); May (G); June (H) (from Friedland et al. 1998*a*).



maximum rate and then decreases at high temperatures (Brett 1979), thus making post-smolt growth-survival mechanisms temperature dependent. As described by Friedland et al. (1998*a*), post-smolts from the Figgjo and North Esk advected passively into the Norwegian coastal current would be affected by prevailing temperature conditions in a given year. In years where water temperatures were high enough to support rapid growth, the juvenile fish would be expected to attain body sizes large enough to avoid predation and survival for the cohort would be enhanced. Conversely, lower temperatures would depress growth and survival. This represents the most direct effect sea surface temperature distributions could have on post-smolts. Other factors, which covary with sea surface temperature trends, may be impacting growth and survival through indirect mechanisms. Contrasts in temperature regime are indicative of differences in weather patterns for a region. Since post-smolt growth is sensitive to changes in photoperiod (Forsberg 1995), the frequency of storms and changes in cloud cover could conceivably affect growth.

Production mechanisms

Primary production and the forage base for salmon post-smolts undoubtedly vary in association with temperature conditions. Recent findings with Pacific salmonids point to the importance of diet in the recruitment process, thus relating quality and abundance of prey to growth and survival (Healey 1991; Brodeur et al. 1992; Perry et al. 1996). Prey availability is often related to oceanographic processes and structural features in the water column (Levings 1994). Juvenile salmonids have been shown to modify their diet in response to feeding opportunities created by the concentration of food along fronts (Brodeur 1989; St. John et al. 1992) or restrictions imposed by thermal structure (Reddin 1985; Pearcy et al. 1988). It has also been hypothesized that variation in ocean productivity acts on post-smolts by shifting predation pressure from other species onto the post-smolts (Fisher and Pearcy 1988).

As a highly migratory species, salmon depend upon a number of orientation cues to successfully orient during their marine migration. The conditions first encountered by post-smolts may force additional swimming as the fish respond to migration cues (Salminen et al. 1994), thus creating energy deficits for the fish as they swim harder to avoid undesirable thermal conditions. In a more extreme case, post-smolts may face potentially lethal thermal conditions when they attempt to migrate from river to ocean environments, again underscoring the importance of climate variation (Narayanan et al. 1995).

Maturation schedules

Cohort differentiation

The linkage between maturation and climate can be seen in the relationship between stock abundance of North American Atlantic salmon stocks and winter temperature conditions in the northwest Atlantic area. Friedland et al. (1993) developed a composite catch time series of the North American stock complex during which catches were generally unrestricted by management measures and is thus taken as representative of stock size (Fig. 6A). This time series differs from the European catch time series in two important

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Fig. 6. Total nominal landings for North American stock complex without Greenland catch, NA, with the North American origin catch from Greenland added to the total, NA and GRE, and a North American estimate if the Greenland Fishery did not exist, NA Estimate (A). North American catch estimate compared to the first principal component of winter habitat area and habitat index for January (B). Data are smoothed (from Friedland et al. 1993*a*).

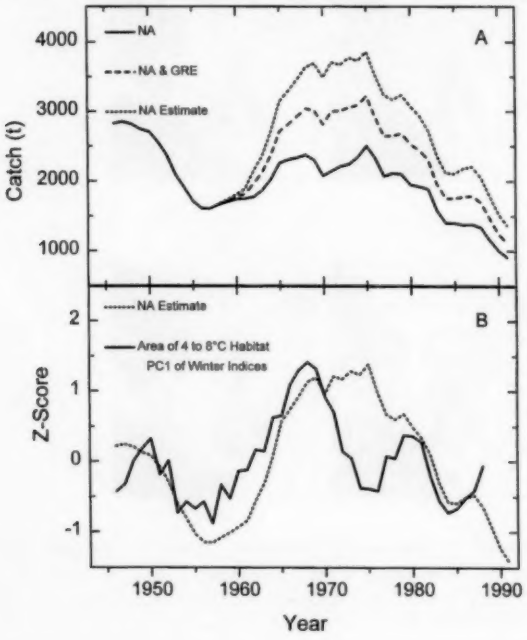
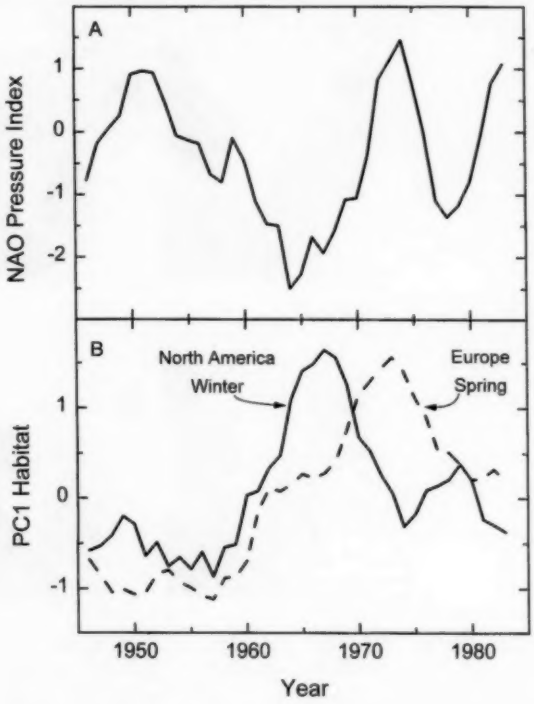


Fig. 7. North Atlantic oscillation pressure difference index between the Azores and Iceland (A). First principal component for North American winter habitat and European spring habitat (B). Data are smoothed (from Friedland et al. 1993).



ways. First, the differences in regional catches in North America are not as pronounced as in the European data (Fig. 3A). Second, the North American series contains a much higher proportion of nonmaturing (2SW) salmon in the catch. Therefore, this series is greatly affected by variation in maturation schedules for the contributing stocks to a much greater degree.

Total stock abundance was correlated to an index of winter thermal habitat in the northwest Atlantic. Winter thermal habitat, as represented by the first principal component of monthly 4–8°C thermal habitat for the months January–March, showed decadal trends similar to the estimate of stock abundance (Fig. 6B). A more refined analysis confirms this relationship by comparing the abundance of North American nonmaturing (2SW) stocks and winter thermal habitat; subsequently this relationship was used as the basis of management in mixed stock fisheries (Reddin et al. 1993).

The distribution of sea surface temperature data that is critical for Atlantic salmon appears to be related to the North Atlantic atmospheric oscillation. The position of the westerlies over the North Atlantic and the position of the Iceland low-pressure center define the oscillation (Dunbar and Thomson 1979; Mann and Lazier 1991). When the westerlies are in their northerly position, high pressure occurs in the north central Atlantic Ocean. When the westerlies are at their southern extreme, cold air from the Arctic invades the Labrador Sea and Greenland area. The atmospheric pressure difference between the Azores and Iceland during winter indicates the magnitude of the oscillation. Friedland et al. (1993) found that the oscillation is in negative phase with the area of 4–8°C winter habitat for North American stocks (Fig. 7). In comparing the distribution of 4–8°C water when the oscillation was high versus a period when it was low, it was found that the greatest differences occurred in the area of East Greenland and the Davis Straight area of the Labrador Sea (Fig. 8).

Migrational models

Friedland et al. (1998*b*) propose a hypothesis that migration may be a significant determinant of maturation in Atlantic salmon, which they support with data on elemental composition of otoliths, maturation trends, and the relationship between population abundance and ocean climate. Though the hypothesis is specified for southern North American salmon stocks, ones with age structures that include fish that mature at both 1SW and 2SW, it is intended as a general hypothesis applicable to all stocks. The principal aspect of the hypothesis is that fish that migrate more northerly as post-smolts are differentially affected by overwintering conditions and may also find themselves in a location, after winter, where they fail to receive cues related to sensing their home rivers. As a result, these fish feed and grow and join feeding migrations, as in the case of these

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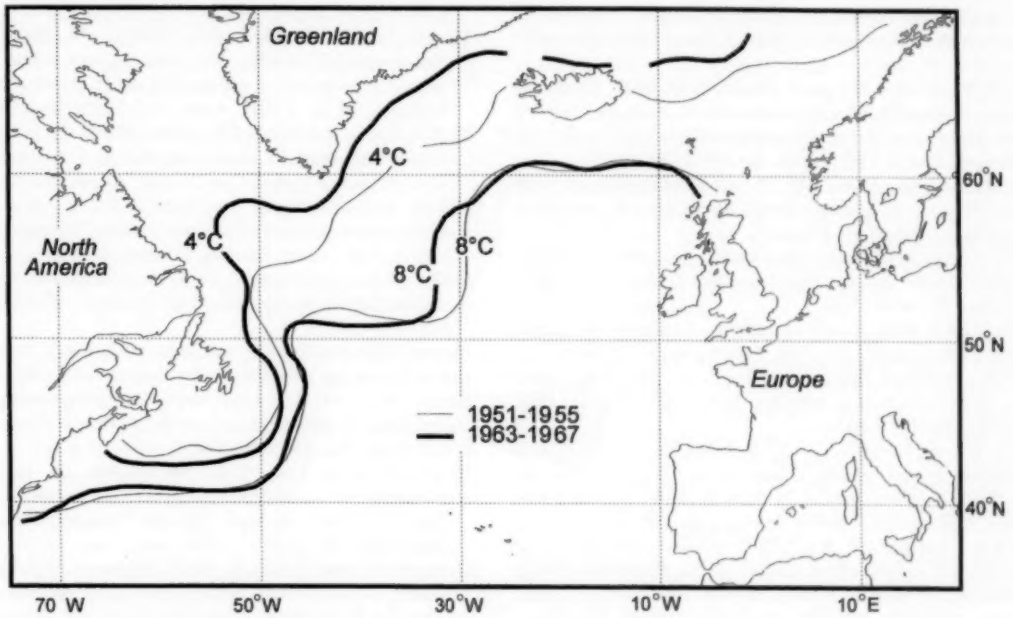
Fig. 8. Map of North Atlantic ocean indicating areal extent of 4–8E°C water during two periods: 1951–1955 when the North Atlantic oscillation index was high and 1963–1667 when the index was low (from Friedland et al. 1993).



North American fish, in feeding areas in the Labrador Sea. As a consequence, they regress in their maturation state. Alternatively, fish that make a more southerly post-smolt migration experience different overwintering conditions and are closer to home rivers after winter. They are more likely to receive cues associated with their natal rivers, develop sexually, and invoke other behaviors to navigate home. This segment of the salmon's migration is not well known; however, it is clear that homing salmon change behavior in response to cues associated with natal rivers (Hansen et al. 1993). Though not well studied, there is precedence for relating migration to maturity. Woodhead (1959) found that immature cod in the Barents Sea which follow different migration routes, showed different patterns of sexual development.

The relationship between the abundance of North American 2SW spawners and the areal extent of thermal habitat during their first seawinter is consistent with the migration–maturation hypothesis described above. A number of competing theories have been proposed to explain the relationship between winter thermal habitat and abundance (Friedland et al. 1993). Ideas based on competition or survival mechanisms have always been difficult to rationalize because post-smolts nearly achieve adult size by their first seawinter and thus are not as likely to experience predation rates as high as juvenile fish. Likewise, it is equally difficult to support mortality due to starvation. On the other hand, the concept that ocean climate simply influences a segment of the stock to take a more northerly post-smolt migration and thus not sexually mature after the first seawinter, offers a consistent, albeit still inconclusive, explanation for the observed phenomena.

Conclusions

An improved understanding of the linked mechanisms involved in controlling decadal climate response in the North Atlantic is emerging (Latif et al. 1996). Furthermore, climate predication models that could be used to feed back into biological models are under development (Griffies and Bryan 1997). As we learn more about the biological response of Atlantic salmon to environmental variation, we should be able to develop a unified model of survival and maturation for the marine phase that could be used to complement freshwater production models. Management policy that is predicated on freshwater production trends and political challenges and ignores decadal scale trends in ocean productivity is doomed to failure (Lawson 1993). It is critical that both environments be linked and that the life history of the salmon be viewed in its totality.

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One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture

Mart R. Gross

Abstract: Today, over 94% of all adult Atlantic salmon (*Salmo salar*) are in the aquaculture niche and wild numbers continue to decline while aquaculture numbers increase. The developmental and evolutionary forces in the aquaculture or "domestic" niche are so unlike those in the wild niche that two distinct biologies are being created from the original Atlantic salmon species. We may now need to recognize a new biological entity — *Salmo domesticus* — and treat it as an "exotic" when it escapes into the wild. Escapement therefore raises important concerns about ecological and genetic impacts, both within and outside the native range of *Salmo salar*. This paper explains why escaped domestic Atlantic salmon have had an impact on wild Atlantic salmon populations and now threaten Pacific salmonids as well. A polarization of views between aquaculturists and environmentalists will not resolve the problems. The three interest groups in fisheries — aquaculture, biodiversity, and capture — must begin to work together if we are to take up the challenge of preserving biodiversity and if aquaculturists, who hold the future of Atlantic salmon in their hands, can be expected to willingly prevent further impacts from their industry.

Résumé : Aujourd'hui, 94 % des saumons de l'Atlantique (*Salmo salar*) adultes sont issus de l'aquaculture, et les effectifs de saumons sauvages continuent de décroître tandis que les effectifs provenant de l'aquaculture augmentent. Les forces agissant sur le développement et l'évolution des saumons d'aquaculture, ou des saumons « domestiques », sont si différentes de celles agissant sur les saumons sauvages que deux biologies distinctes se sont formées à partir du saumon atlantique d'origine. Nous pouvons aujourd'hui considérer une nouvelle entité biologique — *Salmo domesticus* — et la traiter comme une entité exotique quand elle s'échappe dans le milieu naturel. Le fait que des saumons d'aquaculture s'échappent dans le milieu naturel soulève des inquiétudes importantes au chapitre des impacts écologiques et génétiques tant à l'intérieur qu'à l'extérieur de l'aire de répartition naturelle de *Salmo salar*. Le présent article explique pourquoi les saumons atlantiques domestiques évadés ont eu un impact sur les populations sauvages de l'espèce et menacent maintenant aussi les salmonidés du Pacifique. Les problèmes ne trouveront pas de solution dans une polarisation des positions des aquaculteurs et des environnementalistes. Les trois groupes d'intérêts du secteur des pêches — les aquaculteurs, les personnes qui se préoccupent de la biodiversité, et les pêcheurs — doivent commencer à collaborer si nous voulons réussir à préserver la biodiversité et si nous voulons faire en sorte que les aquaculteurs, qui ont l'avenir du saumon atlantique en leur pouvoir, en arrivent à freiner volontairement les impacts de leur industrie.

[Traduit par la Rédaction]

Introduction

Although the wild Atlantic salmon (*Salmo salar*) entered commercial aquaculture only 25 years ago (e.g., Boghen 1995; Saunders 1995; Anderson 1997), its biomass in aquaculture already exceeds that in its native range. This shift in abundance and distribution raises important questions about the evolutionary fate of Atlantic salmon and about the potential for ecological and genetic impacts on wild populations both within and outside the native range. The purpose of this paper is to discuss the implications of aquaculture for the future of the Atlantic salmon and other species in the wild.

My laboratory initiated studies of wild and cultured salmon in the early 1980s when government "enhancement" led to a massive hatchery program for Pacific salmon in western North America (e.g., van den Berghe and Gross 1984, 1986, 1989; Gross 1985, 1991; Fleming and Gross 1989, 1990, 1992, 1993, 1994). By the late 1980s we brought this knowledge to a Norwegian program comparing wild and cultured Atlantic salmon (e.g., Fleming et al. 1994, 1996). With Atlantic salmon now cultured in Pacific waters, we are back studying the possible impacts of escaped Atlantic salmon. Regrettably, research on wild–cultured interactions operates in a politically charged and antagonistic environment where there are those who favor aquaculture and those who favor the wild fish. Moreover, their lack of biological knowledge and the political implications of conflict have largely paralyzed government agencies with a mandate to foster both. As a consequence, the needs of specific research programs on the interactions between wild and cultured fish are often overlooked.

This paper underscores the necessity for cooperation among all interest groups in interpreting and understanding the research outcomes from such programs and in assessing how we might best manage these outcomes to foster aquaculture, natural biodiversity, and capture fisheries. The paper has four sections. By beginning with a review of the

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M.R. Gross. Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada. e-mail: mgross@zoo.utoronto.ca

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abundance and distribution of wild and cultured salmon and the ecological and life history differences of their niches, we realize that cultured fish have become a distinct evolutionary lineage. Therefore, it may now be time to recognize the evolution of "*Salmo domesticus*." The second section raises and reviews the potential impacts of domestic salmon that escape into the habitats of wild Atlantic and wild Pacific salmon. For both cases it is argued that the escaped fish are an "exotic" and therefore the concerns associated with exotic introductions are important (e.g., International Union Conservation of Nature (IUCN) 1997). Section three highlights the importance of "ecorealism" in dealing with the impacts of aquaculture on salmonid biodiversity. Salmonid aquaculture brings both benefits and costs to wild fish populations and it is necessary to maintain a balanced perspective. Finally, section four provides recommendations for future directions which include the collaborative effort of all three sectors in fisheries — aquaculture, biodiversity, and capture fisheries — to solve the challenges of the novel evolutionary and ecological experiment that the recent massive culture of salmon presents.

The evolution of "*Salmo domesticus*"

The wild and aquaculture niches differ greatly in their capacity, distribution, ecology, and life history and an appreciation of these differences is necessary to understand the future directions of the Atlantic salmon as a species.

Niche capacity and distribution

Wild

The native wild niche includes the rivers and northern Atlantic Ocean bound by North America, Scandinavia, and Europe between 40° and 70°N (MacCrimmon and Gots 1979). Prior to human predation and habitat alteration, this niche may have supported 10–24 million adult individuals (50 000–100 000 mt). In the past 50 years, it is unlikely for populations to have exceeded 5–8 million adults (25 000–35 000 mt) (calculations by R. Behnke in Parrish et al. (1998)).

Aquaculture

By contrast, the aquaculture niche is worldwide and extends the native distribution into the Pacific Ocean and Southern Hemisphere (Heen et al. 1993). For example, net pens in the Pacific waters of British Columbia, Canada, were producing almost 4 million adult individuals in 1995 alone (17 000 mt; calculated from 1995 statistics of the BC Provincial Ministry of Agriculture, Fisheries and Food). In the Southern Hemisphere (40° and 60°S), 1995 production in Tasmania reached 1.4 million (6000 mt) and in Chile about 12 million individuals (54 000 mt).[1] Worldwide figures for 1995 estimate some 104 million adult Atlantic salmon living in commercial aquaculture (471 820 mt), with roughly 25% outside the native range. By year 2000, with predicted increases of 40–65% above year 1995 (Anderson 1997), there may be 146–172 million adults in aquaculture.

Relative capacity and distribution

Clearly the aquaculture niche dwarfs the wild niche in both current and historic capacity. In 1995, well over 94% of all Atlantic salmon adults were in aquaculture. Even at maximum carrying capacity, the wild niche will support only 10% of the adults projected for the aquaculture niche by year 2000. The spatial and numeric distributions in aquaculture are also unique. More than two farmed Atlantic salmon live in the Southern Hemisphere for every wild individual in the native Northern Hemisphere; about three farmed salmon are in the Pacific drainage for every one wild individual in the Atlantic drainage. Within the native range, Norway has roughly 100 000 wild spawners (Jonsson and Fleming 1993) or 1.5% of the world's wild Atlantic salmon, but 59 million or 57% of all the world's adult Atlantic salmon (wild and 1995 cultured).

Ecology and life history

Ecological and life history differences found within the wild and aquaculture niches are summarized in Fig. 1. These differences give rise to the developmental and evolutionary forces, Fig. 2, which pry apart the biology of the species. Some of the resulting differences are summarized in Table 1.

Evolution of *Salmo domesticus*

Genetically based evolutionary changes move the fish towards "domestication," thereby adapting the Atlantic salmon to the aquaculture niche while simultaneously maladapting it to the wild niche. The complexity and power of selection within the aquaculture niche is seen, for example, in the rapid response across generations of tameness toward human handlers, while evolving increased aggression to each other. After a few generations in the high-density niche of aquaculture, farmed juveniles aggressively out-compete wild juveniles in competition experiments and hybrids show intermediate aggression levels (Einum and Fleming 1996). Fleming et al. (1994, 1996) show other remarkable morphological and behavioral differences between first and fifth generation Norwegian farmed salmon.

Salmon breeders commonly use artificial selection to improve performance traits (Gjerde 1993). The economic benefits of selective breeding include reduced production costs, more rapid turnover time, better quality product, and thus greater market acceptance. The Norwegian program, which has successfully increased growth rate, decreased early maturity, and increased disease resistance, now provides egg stock to many countries of the world. Future production of Atlantic salmon may include more substantial genetic changes, such as the current availability of triploid and transgenic Atlantic salmon (Donaldson 1997).

The inevitable outcome of the natural and artificial selection forces within the aquaculture niche is the increasing divergence within the Atlantic salmon species into distinct biologies reflecting the distinct niches of wild and aquaculture (Fig. 2). Both intentionally and unintentionally, a new life form of Atlantic salmon is emerging from the aquaculture niche. Farmed salmon may eventually become

[1] FAO (1997*a*, 1997*b*) aquaculture statistics are in metric tons (mt) for the 14 countries producing Atlantic salmon in 1995, the most recent statistics available. Throughout this paper, tonnage is converted to the number of individuals by assuming a mean fish body weight of 4.5 kg. This provides a rough estimate that is useful for comparison purposes.

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Fig. 1. The behavioral ecology and life history of Atlantic salmon in its two niches: wild and aquaculture.

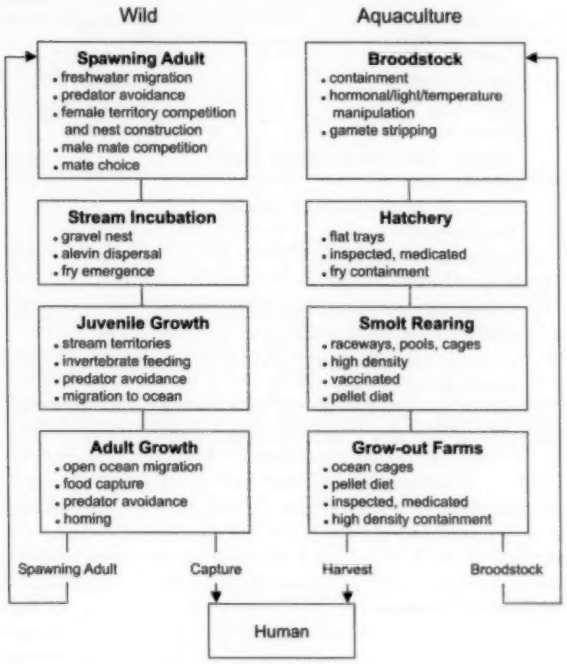
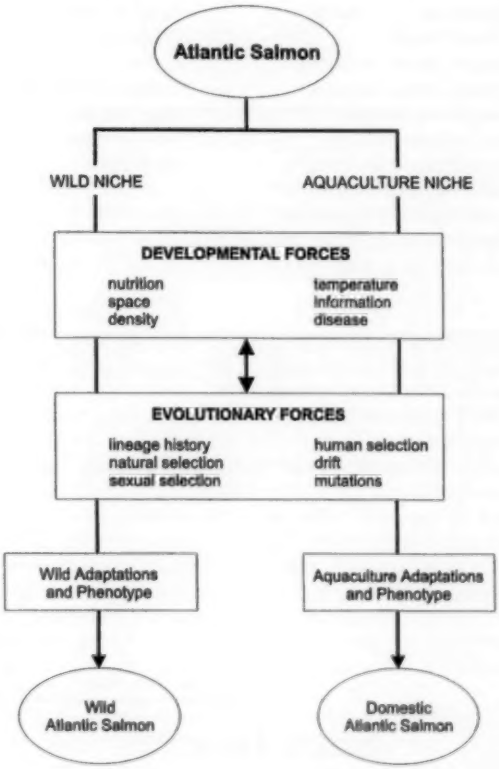


Fig. 2. Developmental and evolutionary forces affecting the Atlantic salmon gene pool in the wild and aquaculture eventually result in a wild and a domestic organism, with distinct evolutionary lineages.



obligate parasites, entirely dependent upon humans for survival; already humans shoot their predators, apply medicines to fight their diseases and parasites, provide special foods, and flush the niche with clean water to remove wastes, etc. The process and result are similar to the historic domestication of chickens, cows, pigs, sheep, and other animals and plants that has occurred over the past thousands of years but through technology it has become more rapid. While this paper considers two extremes in Atlantic salmon biology, wild and farmed, there are of course gradations between these two that must also be recognized (Fig. 3). In time the fisheries community may want to give new labels to these new life forms. To begin, we should recognize the existence of farmed Atlantic salmon as *Salmo domesticus*. Such a distinction will help us realize that in spite of the large biomass of *Salmo* in aquaculture, the wild species *Salmo salar* is endangered. Moreover, the domestic Atlantic salmon is an "exotic" when it leaves its aquaculture niche and enters either the native range of wild *Salmo salar* or into new areas of the globe.

Biological implications of domestic salmon in the wild

The creation of a domestic fish species or population as well as its distribution into novel places of the world raises important concerns about potential impacts on native wild fish through a "collision of biologies" (Fig. 4). The potential for a genetic and ecological collision is related to the magnitude of escapement and the degree of direct and indirect interaction in the field. We first consider these concerns from a theoretical perspective, evaluate the magnitude of escapement, and address what is known and likely in the Atlantic and Pacific oceans.

Theoretical concerns

The specific impacts of exotic introductions are usually difficult to predict (e.g., Moyle and Light 1996; Shigesada and Kawasaki 1997). At a global level, exotic introductions have shown many significant negative impacts and invading aliens are considered second only to habitat loss as the major threat to native biodiversity and the integrity of natural communities (IUCN 1997). The "tens rule" suggests that about 10% of introduced exotics will establish themselves (Williamson 1996). Among established exotic fish in the United States, about 50% are known to have had harmful effects, usually through ecological impacts (US Congress Office of Technology Assessment 1993). This suggests a roughly 5% probability of negative impact from escaped and invading domestic Atlantic salmon (0.10 establishment × 0.50 harm). While a 5% probability may appear low, we should not underestimate the powerful harm that can occur. Some of the greatest ecological disasters in North America have resulted from invading exotic fish including salmonids (e.g., Mills et al. 1993, 1994). Of the 86 endangered fish

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Table 1. Some genetic and developmental differences between cultured (farmed) and wild Atlantic salmon.

Genetic		Developmental	
Confirmed[a]	Suspected[b]	Confirmed[a]	Suspected[b]
Increased growth rate	No ejaculation	Lower stamina	Gut length
Increased age of maturity	Reduced male courtship	Smaller eggs	Diet preference
Increased weight	Higher hatchery survival	More eggs	Stream knowledge
Increased disease resistance	Higher temperature tolerance	More fat	Body odor
Decreased stress response	Shallower depth preference	Smaller rayed fins (parr and adult)	
Lower genetic diversity	Larger testes	Smaller heads on parr	
Allele frequency change	Juvenile color	Narrower caudal peduncle on parr	
Malic enzyme allele change	Adult color	Bulkier body on adult	
Reduced predator response		Distorted jaw on adult	
Increased juvenile aggression		Longer head on adult	
Increased tameness		Longer adipose fin on adult	
Lower survival in wild		Smaller hearts in females	
		Decreased juvenile color	
		Decreased adult color	

[a]Aksnes et al. 1986; Cross and King 1983; Einum and Fleming 1996; Ferguson et al. 1997; Fevolden et al. 1991, 1993; Fleming et al. 1994; Friars et al. 1990; Gjedrem 1979; Gjedrem et al. 1988, 1991; Gjerde 1984; Jonsson et al. 1996; Ruzzante 1994; Ståhl 1987; Verspoor 1988; Youngson et al. 1991.
[b]Author's observations.

Fig. 3. A "taxonomic picture" of the Atlantic salmon "species."

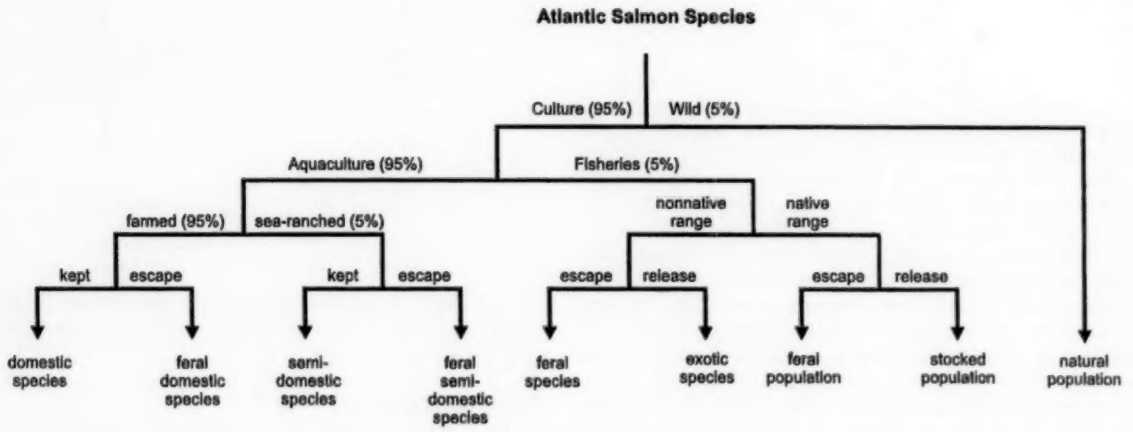

Fig. 4. The genetic and ecological concerns associated with domestic Atlantic salmon escaping from aquaculture and entering the wild.

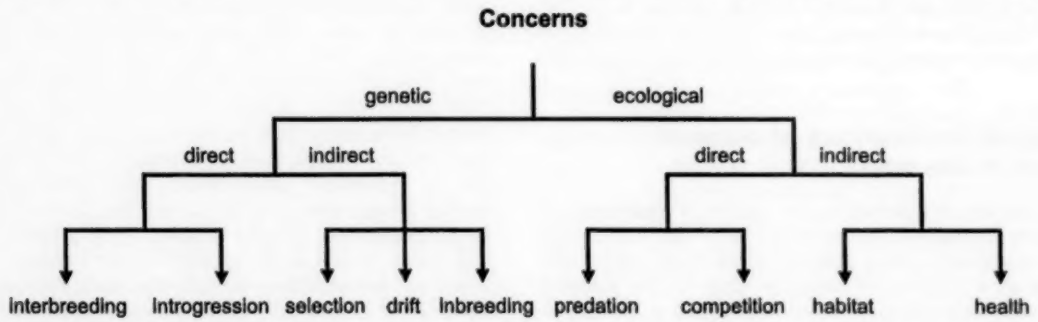

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Table 2. Marine captures of escaped farmed Atlantic salmon in the northeastern Pacific Ocean from 1987 through 1997 (from annual reports of Thomson and McKinnell (1993–1997); and personal communication for 1997 from A. Thomson, Atlantic Salmon Watch B.C.).

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	Mean
Alaska	–	0	0	1	7	2	27	27	23	135	79	30
B.C.	1	106	8	2	31	349	4543	1037	648	671	2623	1002
Wash.	–	6	52	446	970	157	179	338	125	112	2172	456
Total	1	112	60	449	1008	508	4749	1402	796	918	4874	1488

species in the United States, 51% are impacted negatively by exotics, 9% have exotics as their major cause for endangerment, and 6% are endangered due to exotics (Lassuy 1995).

While many authors have called attention to concerns of escaped farmed fish within their native ranges (e.g., Hanson et al. 1991; Hindar et al. 1991; Krueger and May 1991; Saunders 1991; Heggberget et al. 1993; Utter et al. 1993; Allendorf and Waples 1996; Fleming et al. 1996), the potential impacts and concerns also apply outside the native wild range. Escaped farm fish can directly reduce the genetic adaptiveness of wild fish by interbreeding and thus perturbing gene complexes or by introgressing and thus replacing the wild gene pool by a cultured gene pool (Fig. 4). Escaped farmed fish can also indirectly impact the genetics of wild fish by generating new forms of selection or by reducing wild population size so that genetic drift or inbreeding decreases genetic adaptiveness. Ecologically, escaped farmed fish can reduce the adaptiveness of wild fish directly by competing for resources such as food or space, or by preying on wild fish at their early life stages, or indirectly through habitat modification such as disturbing spawning redds, or introducing new or higher intensities of disease.

Escapement of domestic salmon

The movement of domestic individuals into the wild is not uncommon. Recent estimates from the salmon farming industry in British Columbia suggest that up to 2% may enter the wild each year (Alverson and Ruggerone 1997). Losses can occur in large pulses or through small leakages. For example, in 1988 a single winter storm along the middle coastal region of Norway released about 700 000 individuals into the Atlantic Ocean (Gausen and Moen 1991). In the Pacific, 101 000 Atlantic salmon were released into Puget Sound, Washington State, on 2 July 1996 and over 360 000 on 18 July 1997 from mishaps at single farms (Thomson and McKinnell 1997; personal communication from A. Thomson, Atlantic Salmon Watch B.C.). Escapement into the wild is known to occur at all life stages from yolk-sac fry up to and including adults (e.g., Lough et al. 1997).

Native range

Within the native range of wild Atlantic salmon, significant numbers of free-living farmed fish are now found. Examples include: (1) the salmon feeding grounds in the Northeast Atlantic Ocean where 25–48% of individuals are escapees from fish farms (Hansen et al. 1993); (2) Norwegian wild rivers, where 20–30% of all breeding adults are escapees from farms; this rises to over 80% in some rivers (Skaala and Hindar 1997); and (3) the Magaguadavic River in New Brunswick, Canada, where 51–68% of the smolts migrating to the ocean are losses from three hatcheries that produce Atlantic salmon smolts for aquaculture (Stokesbury and Lacroix 1997).

Pacific drainage

In the North American Pacific drainage, where the Atlantic salmon is farmed in only small areas of Washington State and British Columbia, the marine commercial and recreational fishery report incidental captures averaging 1488 per year over the past 10 years with a trend toward increasing numbers (Table 2; McKinnell et al. 1997). The State of Alaska prohibits Atlantic salmon farming; however, incidental captures of Atlantics are made along the coast of Alaska and the Aleutian Islands; they probably originate from farms in lower British Columbia and upper Washington State. Recently, an Atlantic salmon with a full stomach of pteropods was captured in a bottom trawl in the Bering Sea (U.S. National Marine Fisheries Service; personal communication from A. Thomson, Atlantic Salmon Watch B.C., 18 November 1997).

Escaped Atlantic salmon are also found in the freshwaters of the Pacific region. In British Columbia, two lakes are used to raise Atlantic salmon juveniles in net pens; escaped juveniles were found in both lakes and in one a variety of stages including fry, parr, pre-smolts, and smolts (Lough et al. 1997). Elsewhere, an estimated 20 000 pre-smolts were accidentally spilled into a stream from a hatchery transport truck and at a later time 860 live parr were electrofished from the stream. Some were discovered in the stomachs of cutthroat trout in a lower lake and about 55 were found the next spring in the lake and at its outlet. The number of adult Atlantic salmon that are leaving the Pacific ocean and entering freshwater rivers in Washington and British Columbia is rapidly increasing (Fig. 5) and over 50 rivers have been documented as having adult Atlantic salmon.

Amount

While some movement of Atlantic salmon from the aquaculture niche into the wild will be inevitable, the amount will vary with facilities (e.g., net pen vs. land-based containment), location (e.g., ocean exposure vs. sheltered bays), and societal regulations (e.g., laws, insurance premiums). The total loss will also depend on the total number of fish in the aquaculture niche. There is, for instance, a positive 7-year correlation between the number of smolts placed into Norwegian net pens and the number of escapees that are later captured in ocean fisheries and Norwegian rivers (Lund et al. 1997).

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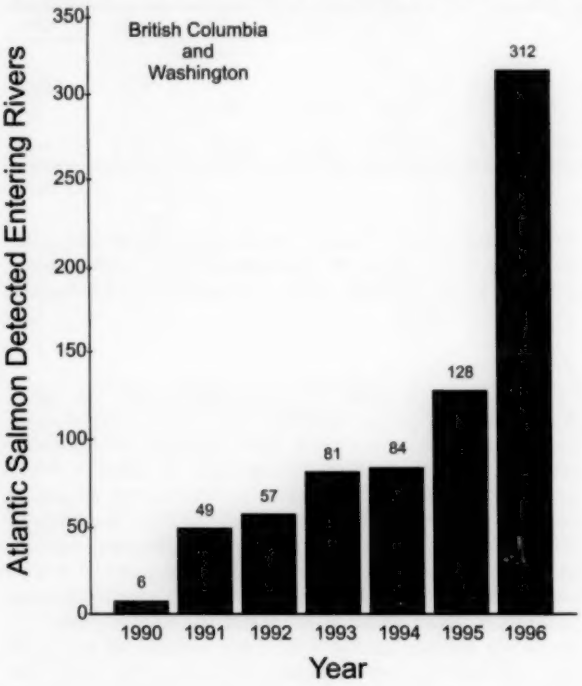
Fig. 5. The number of farmed fish documented in rivers of British Columbia and Washington State from 1990 through 1996 (Atlantic Salmon Watch Program B.C., courtesy of A. Thomson).



Assuming 146–172 million adult Atlantic salmon in the aquaculture niche by year 2000 and a 1–2% escapement, an estimated 1.5–3.4 million adults may enter the wild each year. The number of escapees therefore probably exceeds 50% of all wild adult Atlantic salmon in the world. Roughly 75% of these escapees will be in the native wild niche of the Atlantic drainage and the remainder in non-native waters of the Pacific drainage.

The Atlantic ocean experience

There is mounting evidence that many of the concerns about a collision of biologies are materializing in the native range of Atlantic salmon in the Atlantic drainage. First, Atlantic salmon that have escaped from farms are known to be spawning throughout the native range including rivers in Norway, Scotland, Ireland, Iceland, and Eastern Canada (Table 3). Although their spawning success is less than that of wild individuals, their sheer numbers can result in a relatively high total contribution to the gene pool within rivers. For example, Crozier (1993) demonstrated a shift in the gene pool of a wild Atlantic salmon population in Ireland after escapement from a farm raising a Scottish aquaculture strain. In the River Vosso, one of Norway's historically famous wild salmon rivers, escaped farm fish now contribute about 44% of the total genes (Skaala and Hindar 1997). In an experimental study involving genetic marking of farmed and wild fish, farmed fish contributed 21% of the total genes in the River Imsa, Norway. Most of the genetic contribution was through hybridization, probably between wild males and farmed females (Fleming et al. 1997). In the Magaguadavic River, New Brunswick, Canada, an estimated 55% of the redds are from farmed fish (Carr and Anderson 1997). These significant influxes of aquaculture genes into wild populations will shift the wild populations from local optima thus disrupting life history adaptations and maladapting the populations. As the genetic differences across wild populations are homogenized, the capacity for evolution of the wild fish is reduced. While empirical observations from a number of salmonid species suggest that gene flow levels of this magnitude will result in poorer performance (Hindar et al. 1991), no direct study has yet been done on domestic and wild Atlantic salmon.

Second, ecological impacts occur through food and space competition, reproductive habitat perturbation, and disease transfer. For example, Ferguson et al. (1997) placed three lines of fish — farmed, wild, and hybrid — into an Irish river to study their behavior and growth. The farmed fish behaviorally displaced the wild fish into downriver sections where feeding rates are probably lower; the farmed fish grew fastest, the hybrids intermediate, and the wild fish slowest. In Norway, Fleming et al. (1997) found that the offspring of farmed fish that bred in the River Imsa grew faster than the offspring of wild fish, with hybrids having intermediate growth. A common reproductive habitat perturbation occurs during the spawning season when escaped farmed fish, lacking information about the wild rivers, typically arrive later at the spawning grounds. This late arrival results in farmed fish digging up the gravel that already contains the nests of wild females and replacing the wild eggs with their own (e.g., Webb et al. 1991).

The impact of disease and parasite transfer has been one of the strongest to date. For example, *Gyrodactylis salaris* was carried by farmed Swedish smolts out of the Baltic Sea drainage and into the eastern Atlantic drainage, where it is known to have extirpated over 35 wild populations in Norway (Johnsen and Jensen 1991). Atlantic salmon in the eastern Atlantic drainage are more susceptible to this disease than those in the Baltic Sea drainage, thus the Baltic aquaculture fish act as carriers of the disease, not becoming ill themselves but infecting less resistant populations. The transfer may have occurred during enhancement practices. *Aeromonas salmonicida* or furunculosis was carried by Scottish smolts to Norwegian aquaculture and probably spread through escapees to infect hundreds of wild populations (Johnsen and Jensen 1994). Finally, it is thought that sea lice are being transferred from farms where sea lice remain a common problem (Scottish Office Agriculture 1997). It was recently found that sea lice are denser on 1 sea-winter escaped farmed fish than 1 sea-winter wild fish (Jacobson and Gaard 1997). These sea lice may contribute to increased wild stock mortality, reduced seawater growth, and premature return of adults (e.g., Todd et al. 1997).

Although it is difficult to quantify or partition the impacts on wild Atlantic salmon by escapement from the aquaculture niche (e.g., Fig. 4), it can no longer be reasonably questioned that major impacts do occur. Over the last decade, the primary ecological impact on wild fish health is through the transfer of diseases and parasites. While new diseases and parasites will surely appear, the current problems are now better controlled in the aquaculture niche (e.g., Aarflot 1995; Bruno and Poppe 1996; except perhaps for sea lice; also, re-

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Table 3. Observations on the occurrence, survival, and biology of cultured (farmed) Atlantic salmon in the wild.

Character	Observation	Reference
Abundance	25–48% of salmon on feeding grounds in NE Atlantic Ocean	Hansen et al. (1993)
	50–80% of spawners in River Vosso, western Norway	Skaala and Hindar (1997)
	20–30% of all Norwegian spawners	
	51–68% of all smolts leaving Magaguadavic River, New Brunswick have escaped from hatcheries	Stokesbury and Lacroix (1997)
	Over 2000 marine captures and 140 adult freshwater captures per year in NE Pacific Ocean between 1993 and 1997	Atlantic Salmon Watch — A. Thomson, peronal communication
	Postitive correlations between smolts placed into Norwegian cages and percent capture in fisheries and in Norwegian streams (7-year assessment)	Lund et al. (1997)
Survival	Two-fold lower marine survival (sea-ranched)	Jonsson et al. (1991)
	20% lower juvenile survival in streams	Ferguson et al. (1997)
Size, feeding, and growth	Escaped smolts larger in size when migrating from Magaguadavic River, New Brunswick	Stokesbury and Lacroix (1997)
	Experimentally introduced farmed strain and hybrids grow faster than wild juveniles in rivers in Ireland	Ferguson et al. (1997)
	Experimentally introduced farmed strain and hybrids grow faster than natives in Norwegian river	Einum and Fleming (1997)
	Naturally spawned farmed and hybrid offspring grow faster than native juveniles in Norwegian river	Fleming et al. (1997)
	Adult farmed females entering Norwegian river are 10% smaller in size than wild females	Lura and Sægrov (1991)
	About 7% of marine captures of escaped farmed fish in NE Pacific Ocean have prey in stomach	McKinnell et al. (1997)
	About 35% of marine captures of escaped Atlantic salmon in Scottish marine waters have prey in stomach	Hislop and Webb (1992)
	Farmed and hybrid offspring from natural breeding are scattered throughout Norwegian river during juvenile growth	Fleming et al. (1997)
Reproductive behavior	**Norway**	
	Later maturity and spawning than wild females	Heggberget (1988)
	Earlier maturity and spawning than wild females (3.5 weeks)	Lura and Sægrov (1991)
	Utilize similar spawning habitats	Økland et al. (1995); Fleming et al. (1997)
	Males competitively inferior	Fleming et al. (1997)
	Females show less breeding behavior and are less efficient at nest covering; males are less aggressive and court less	Fleming et al. (1996)
	Iceland	
	Adults enter rivers later and spawn later than wild stock	Gudjonsson (1991)
	Scotland	
	Farmed adults stay lower in river and spawn later	Webb et al. (1991)
	Eastern Canada	
	Adults enter river later than wild fish	Carr et al. (1997)
Reproductive success	Farmed progeny hatch and initiated feeding earlier in Norwegian streams	Lura and Sægrov (1991)
	Females carry more unspawned eggs, have more nest destruction, greater egg mortality, and overall less than 1/3 the success of wild females (Norway)	Fleming et al. (1996)
	Males have fewer spawnings, often do not ejaculate, and overall have less than 3% the success of wild males (Norway)	Fleming et al. (1996)
	Successful spawning	Lura and Sægrov (1991)
	Unfertilized eggs	Lura and Sægrov (1991)
	Successful spawning in an eastern Canadian river in 1993	Carr and Anderson (1997)
	55% of redds are of farmed origin in an eastern Canadian river	Carr and Anderson (1997)

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Table 3 (*concluded*).

Character	Observation	Reference
Reproductive interactions	Interbreeding of a Scottish farmed strain with wild fish in an Irish river and shift in wild gene pool	Crozier (1993)
	Farmed fish producing over 44% of the genes in the River Vosso, western Norway demonstrating that gene pool is being replaced by farmed strain	Skaala and Hindar (1997)
	Farmed fish contribute 21% of the genes in River Imsa, southwestern Norway, mainly through hybridization, after experimental release	Fleming et al. (1997)
	Farmed fish dig up wild fish's eggs when making their own nest	Webb et al. (1991)
Disease and parasites	Sea lice in farms apparently contributing to increased wild stock mortality, reduced seawater growth, and premature return	Dawson et al. (1997); McVicar (1997); Todd et al. (1997)
	More sea lice on 1 sea-winter escaped farmed salmon than wild salmon in Norwegian sea	Jacobson and Gaard (1997)
	Gyrodactylis salaris carried into Eastern Atlantic drainage from Baltic sea drainage by smolts from Swedish farm, killing over 35 Norwegian wild populations; the latter are more susceptible	Johnsen and Jensen (1991)
	Aeromonas salmonicida (furunculosis) carried to Norwegian aquaculture from Scottish smolts, probably spread by escapees to wild populations	Johnsen and Jensen (1994)

cent outbreaks of ISA — infectious salmon anemia). I suspect that the impact of most concern for wild fish in the future will be genetic, through interbreeding and introgression of aquaculture genes and through increasing drift and inbreeding due to reduced wild population size (due in part to increasing competition and further habitat perturbation). The resulting loss of the wild gene pool may give rise to yet less fit individuals for future evolutionary change and survival in the wild. There is a strong possibility that the magnitude of escapement combined with the biological divergence between the two niches will result in the disappearance of all wild Atlantic salmon populations within areas of aquaculture.

The Pacific Ocean experience

In North America there is strong concern over the increasing numbers of escaped Atlantic salmon discovered in marine and freshwater habitats and their potential impact on native Pacific salmonids. Unlike the situation in the Atlantic native range, no impact has been clearly documented to date (Environmental Assessment Office of British Columbia 1997). This may be because there is only limited research being conducted to study impacts. One significant program is the Atlantic Salmon Watch, which primarily documents the volunteered reportings of the number of marine and freshwater sightings and provides limited biological information (McKinnell et al. 1997).

Additional research on several key concerns should become an immediate priority if net-based fish farming is to continue (Fig. 4). First, direct genetic impacts are possible through hybridization with Pacific species. Four pieces of evidence supporting this contention are (1) European studies show that farmed female Atlantic salmon have increased hybridization rates with salmonids in the wild possibly as a consequence of decreased mate discrimination (e.g., Sægrov 1993; Youngson et al. 1993; Hindar and Balstad 1994); (2) most Pacific salmonids overlap to some degree in spawning season and breeding habitat with those of the Atlantic; (3) experimental crosses by R. Devlin (Department of Fisheries and Oceans, Vancouver, B.C., Canada, personal communication) show that survival to at least the hatch of F1 progeny occurred in 10 of 14 possible crosses between male, or female, Atlantic salmon, and seven native Pacific salmonid species; and (4) precociously mature Atlantic salmon parr have extended breeding seasons and may lack conspecific mates (about 10% of escaped parr collected in a BC river had precociously mature gonads; parr represent alternative breeding tactics — Gross (1996)). While some hybridization is therefore probable, the production of "hybrid swarms" is less likely since the genetic differences between Atlantic salmon and most Pacific salmonids result in low survivorship of F1s.

Second, and of more serious concern, is the indirect genetic impact of Atlantic salmon males attempting to hybridize with females in populations of native salmonids that are locally endangered and close to extinction (e.g., Slaney et al. 1996). Each Pacific salmonid female that has her eggs fertilized by an Atlantic salmon parr or other male has those eggs removed from the gene pool. A population with only a few native females may therefore loose a significant proportion of its reproductive output with even minor hybridization events.

Third, Atlantic salmon may compete extensively with native salmonid species for food and space. Fausch (1998) found that all co-evolved and non-native salmonids experimentally tested had interspecific effects with Atlantic salmon juveniles that were at least as strong as intraspecific effects due to the more aggressive nature of aquaculture salmon. Of special concern are any size differences among juveniles. For example, it has been shown that coho typically dominate Atlantic salmon juveniles because of a size advantage resulting from the coho's earlier hatch (see Fausch 1998). Thus, Atlantic salmon, which hatch earlier than steelhead, may be expected to dominate steelhead. The

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primary impact of interspecific competition was displacing competitively smaller individuals into less preferable habitats (e.g., from pools into riffles or reverse) (also, Gibson 1981; Beall et al. 1989).

Fourth, perturbation of the habitat would be likely because the Atlantic salmon are an "ecological novelty in a naive community" (Townsend 1996) and would most certainly utilize the habitat in ways different from native salmonids.

Fifth, the Atlantic salmon may carry and harbor diseases or parasites to which Pacific salmonids are vulnerable. One possibility is exotic diseases, although in a recent review of the aquaculture industry in British Columbia this was not regarded to be of particular concern (Stephan and Iwama 1997). The greater concern may lie in the loading of disease on Atlantic salmon relative to native species, due to the confines of aquaculture and selection programs for genetic resistance and disease tolerance. Disease amplification through exotic carriers, followed by transmission to and health reduction of native species, is not uncommon in the biological world.

Recipe for successful invasion

An important question is whether the escaped Atlantic salmon could colonize and invade the Pacific region. The establishment of self-reproducing populations of Atlantic salmon may magnify the impact concerns for native salmonids (Fig. 4). A recent analysis by Alverson and Ruggerone (1997) suggests that colonization is unlikely because historical attempts to introduce anadromous populations of Atlantic salmon around the world, including British Columbia and Washington State in the 1920s, have failed (e.g., MacCrimmon and Gots 1979).

I believe, however, that the invasion of the Pacific region by Atlantic salmon is now probable for at least six reasons: (1) ability to survive in the wild — we have discovered that escaped Atlantic salmon are capable of feeding and migrating thousands of kilometres in the Pacific ocean (Table 3). Furthermore, juvenile Atlantic salmon are able to grow and survive in coastal rivers and lakes (e.g., Lough et al. 1997); (2) reproductive capacity in the wild — we know that at least some escaped Atlantic salmon become reproductively mature and enter freshwater rivers. For example, of 20 adult Atlantic salmon that were sampled in British Columbia rivers between 1991 and 1995, 17 (85%) had mature or maturing gonads (McKinnell et al. 1997). Unlike historic attempts at introductions, where human breeders chose the places and times to release embryos or fry, today's Atlantic salmon are free to choose their own habitat and spawning times and make breeding decisions that maximize reproductive success. Since female Atlantic salmon produce several thousands of eggs, it is possible for a single female to initiate a population (although inbreeding may reduce fitness). An anadromous female may find a mate since mature male parr are resident in at least some coastal rivers; (3) naturalization of brood stock — through successive generations of selection and local rearing, the aquaculture industry has developed local brood stocks. Thus, unlike historic introductions, escapees today are probably at least somewhat genetically and developmentally adapted to the Pacific environment. This adaptation should markedly increase the potential for colonization; (4) magnitude, frequency, and geographic extent of seeding — thousands of Atlantic salmon, young and old (fry with yolk sacs to almost mature fish), are escaping annually and throughout the year into both marine and freshwater habitats, in repeated episodes, and over a large geographic range. This means that all combinations of life history stage, seasonal timing, genetic constitution, and environmental conditions are being experienced by escaped Atlantic salmon, increasing the likelihood of a successful fit; (5) open niches — many open niches now exist for Atlantic salmon because native salmonids, especially chinook, coho, steelhead, and cutthroat, the species that seem most similar to the Atlantic salmon, have been dramatically reduced in number and in many cases are locally extirpated (Walters 1995; Slaney et al. 1996). Thus, historically productive salmon streams are unoccupied and large amounts of food and space for rearing and habitat for spawning, exist without competitors; and (6) new niches — the extensive changes brought by humans to the structure of Pacific river systems may result in Pacific salmonids being less competitive and Atlantic salmon better adapted to the new wild niches. Atlantic salmon have a much longer evolutionary history of coexistence with humans and human technology-influenced habitats and therefore may be preadapted to colonize the perturbed niches for which Pacific salmonids are maladapted.

Introducing Atlantic salmon into Pacific waters is an experiment that few conservation-minded biologists would willingly perform today. Historically, eggs or fry were shipped and released into environments where it was not obvious that they could survive. The introduced stock was neither developmentally nor genetically prepared, the releases were relatively small, and the local environment often presented severe biotic competition. Today, the opportunity for invasion is unprecedented and success is probable at the current state of domestication of Atlantic salmon. Whether a new salmonid species in the Pacific drainage would result in a net decrease to all salmonid biodiversity through negative impacts, or instead increase total biodiversity through the addition of a new species, remains an open question.

Ecorealism

Concerns about the interactions between the aquaculture and wild niches of salmon have tended to polarize viewpoints between "developers" of the aquaculture niche and "defenders" of the wild niche (e.g., contrast Kenney's (1997) report "Net Gain" with Ellis' (1996) report "Net Loss"). Developers are often reluctant to accept impacts, while defenders rarely put impacts into a perspective that permits acceptance of any potential benefits. Needham (1995) has thus suggested the need for a touch of "ecorealism" in any aquaculture vs. wild debates.

This paper explains why the escapement of Atlantic salmon from their aquaculture niche presents a concern for the wild niche of Atlantic salmon and for species biodiversity beyond their native range. Historically, the two greatest negative forces on the Atlantic salmon have been the capture fisheries, both commercial and recreational, and habitat alteration and destruction. These forces, expressed through overfishing, misguided stocking, dams, clear-cutting, pulp mills, log booms, terrestrial agricultural,

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mines, cities, storm-water runoff, etc., have resulted in widescale extirpations, depletions, and loss of biodiversity, in both Atlantic and Pacific salmonids, long before commercial salmon aquaculture appeared in the 1970s. While capture fisheries and habitat manipulations will continue to have a negative impact, the concern of many conservation-minded biologists today and into the next century will be the emergence of aquaculture as a third force that impacts on the wild species. Since any one of these three forces can lead to the complete loss of the remaining wild remnants of Atlantic and possibly other salmonids, the three forces combined are cause for significant concern.

Saints or sinners?

Are there any benefits to the wild niche from developing Atlantic salmon in an aquaculture niche? An important potential benefit that is often overlooked is the change that aquaculture is bringing to world salmon markets. First, consumption of farmed Atlantic salmon has now greatly surpassed that of wild Atlantic salmon. Japan, which consumes about 1/3 of the world's salmon, is replacing consumption of many wild salmonid species with fresh-farmed Atlantic salmon (Herrmann 1994). This switch in consumer preference may well occur in other world markets (Harris 1995) resulting in decreasing harvest pressure on wild stocks (Ridler 1995). Second, the increased availability of salmon has dropped the price for wild salmon, thus reducing profitability in the commercial fishery. In western Canada, for example, the value of farmed salmon, of which some 70% are Atlantic salmon, has exceeded the landed value of all commercial wild Pacific salmon harvests since 1995 (British Columbia Ministry of Agriculture, Fisheries and Food 1995, 1996, 1997). Declining harvest values may thus reduce the pressure on wild stocks. Finally, the reduction in commercial value of wild Atlantic salmon has allowed conservation groups and conservation-oriented groups to press forward with further preservation methods. One step has been the purchase of commercial rights. For example, in the north-eastern Atlantic, the buy-out of coastal netting stations around Britain by environmentalists and sport fishers may have resulted in the 30-year high of wild salmon returns to rivers in Scotland during 1995 (Needham 1995). In the northwestern Atlantic, several conservation organizations (North Atlantic Salmon Fund, Atlantic Salmon Federation, National Fish and Wildlife Foundation) were able to purchase the Greenland fishery quotas in 1993 and 1994 (Speer et al. 1997). The North Atlantic Salmon Conservation Organization (NASC), the international scientific body governing salmon fishing with responsibilities for making recommendations concerning Atlantic salmon conservation, was able to recommend in 1996 that all commercial fisheries cease. This recommendation was precipitated by the depleted state of the resource and was politically acceptable due to the reduced commercial value of the resource.

Other potential benefits exist as well. In some cases, the domestic salmon may contribute to conservation through stocking programs (e.g., Shackley et al. 1992). However, this benefit is mitigated by the divergence in biology that has taken place in aquaculture. In addition, the knowledge base being developed about salmon, including their genetics, development, and nutritional needs, may in future be applied to the conservation of the wild niche.

In summary, the creative and productive management of salmonid species and populations will lie in recognizing and accepting four key points. (1) Aquaculture is presenting a serious threat to wild populations and negative impacts are being documented in the native range and may yet occur outside of that range. (2) Aquaculture will not disappear — it is an industry for the future. (3) Aquaculture is not the root cause of the current dismal state of salmonid fisheries and conservation: mismanaged capture fisheries and habitat destruction are the principal culprits. (4) Aquaculture does offer some benefits for wild populations — the most important being the diversion of commercial economic interests.

Recommendations

The development of a new salmonid niche and the evolution of a new lineage present important challenges both today and for the future. The following three recommendations may help us meet those challenges.

1. Develop a new vision for fisheries research and management

We need to develop a new vision for fisheries research and management which recognizes the interdependence of resource usage among all three stakeholders: aquaculturists, the biodiversity community, and those involved in capture fisheries. Aquaculture, the world's fastest growing agribusiness, is necessary to meet the 30% increase in global fish production required for year 2010 (FAO 1997*c*) and can contribute to both biodiversity and capture fisheries if well managed. The biodiversity sector is a relatively new yet rapidly growing segment of society focused on appreciation and preservation of genetic, population, species, and community diversity for both intrinsic and extrinsic values. It preserves the raw material needed by the capture fisheries and the gene pools that are the genetic resources for aquaculture. Capture fisheries are evolving away from an unsustainable commercial harvest to a new optimization based on sustainability and recreational gains (FAO Code of Conduct for Responsible Fisheries 1995), a process encouraged by aquaculture. Developing a vision of interdependence among sectors encourages cooperation rather than conflict and efforts to maximize benefits and minimize costs become a shared goal.

2. Minimize the impact of aquaculture

There is a false sense that aquaculture is "natural" and may look after itself. Instead, it is a complex and technical agribusiness which, like any new industry, is having larger environmental impacts than need occur over the long run. The industry must acknowledge these impacts and take immediate action on a number of issues including stopping the escapement of farmed fish. The FAO Aquaculture Code of Practice (FAO 1997*c*) provides some helpful direction for aquaculture leaders which, when combined with the vision outlined above, could chart a new course for the future. In turn, governments should be willing to support the development of appropriate aquaculture technology including: closed-containment systems to minimize the escapement of

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fish (and other pollutants); disease assessment and prevention; nutrition; and brood stock development. The economic and cultural benefits of such investments are likely to be high.

3. Establish significant biological research programs

We need to launch significant biological research programs to monitor and control the impact of escaped domestic Atlantic salmon. Current support by government agencies and the industries and public they represent are paltry in comparison to the size of the challenge. For example, the Atlantic Salmon Watch program in British Columbia, a valuable source of monitoring data, lacks a significant budget and is partly dependent on a commercial capture industry that is now largely closed. The situation throughout the rest of the world is not any better. It is time for governments to cease minor, poorly funded research initiatives and begin empowering their staff and other scientists to conduct meaningful studies at the scale necessary for the issues.

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Note added in proof: My prediction, page 139, that escaped farmed Atlantic salmon will produce progeny in Pacific waters has apparently now been confirmed (T. Down, B.C. Ministry of Fisheries, observation and collection of free-living juveniles in Tsitika River, B.C., August 1998).

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Population genetics and the conservation and management of Atlantic salmon (*Salmo salar*)

Jennifer L. Nielsen

Abstract: Molecular genetics provides data with temporal and spatial scales unavailable from other disciplines. Patterns of genetic diversity are influenced by adaptive, environmental, and stochastic factors. The rate of change in genetic markers allows investigations of diversity on temporal scales resulting from recent history (hundreds of years) to deep evolutionary time (millions of years). Cryptic spatial population structure is often revealed by molecular markers. Phylogeographic analysis of genes within populations can unite demographics with glaciation, uplift, climatic shifts, or major floods. Historically, the application of genetic markers has been largely limited to analyses of gene frequencies and patterns of diversity. The consequences of genetic rarity are controversial in relationship to endangerment or patterns of extinction. However, it is widely recognized that genes reflect a species' evolutionary past and represent the raw material underlying the diversity of biological expression throughout a species' range. DNA provides the architecture necessary for a species' adaptation and future survival. Conservation of this evolutionary legacy is important considering anthropomorphic manipulation of a species and the environment upon which it depends. In this paper I investigate evolution and genetic variation in Atlantic salmon (*Salmo salar*) based on the current literature. I further discuss conservation and restoration questions using molecular markers.

Résumé : La génétique moléculaire fournit des données à des échelles temporelles et spatiales que ne peuvent atteindre les autres disciplines. Les profils de diversité génétique sont fonction de facteurs adaptatifs, environnementaux et stochastiques. Le taux de variation des marqueurs génétiques permet l'étude de la diversité à des échelles temporelles couvrant l'histoire récente (centaines d'années) ou des temps évolutionnaires très anciens (millions d'années). La structure spatiale des populations n'est pas apparente, et elle est souvent révélée par les marqueurs moléculaires. L'analyse phylogéographique des gènes dans les populations peut faire apparaître des corrélations entre la démographie et les glaciations, les soulèvements de l'écorce terrestre, les changements climatiques ou les grandes inondations. Historiquement, les marqueurs génétiques ont surtout servi à analyser les fréquences des gènes et les profils de diversité. On ne s'entend pas quant aux effets de la rareté des gènes sur la mise en péril ou les profils d'extinction des espèces. Cependant, on convient généralement que les gènes reflètent le passé évolutionnaire d'une espèce et constituent les matériaux bruts qui déterminent la diversité de son expression biologique dans la totalité de son aire de répartition. L'ADN fournit l'architecture nécessaire à l'adaptation et à la survie d'une espèce. La conservation de ce patrimoine évolutionnaire est importante eu égard à la manipulation anthropique de certaines espèces et des milieux dont elles dépendent. Dans le présent chapitre, j'examine l'évolution et la variation génétique du saumon atlantique en me basant sur la documentation existante. Je traite aussi des questions de conservation et de rétablissement en faisant appel aux marqueurs moléculaires.

[Traduit par la Réduction]

Introduction

Population structure based on evidence from molecular genetics is quickly becoming an integral part of the conservation and management of numerous vertebrate species. Because fishes are the most diverse group of living vertebrates, with over 24 600 known species, our knowledge of their diversity has benefitted enormously from the dramatic developments in biochemical techniques over the last two decades. Previously cryptic relationships at both the inter- and intraspecific levels have been addressed using molecular genetic techniques for many groups of fishes, including the Atlantic salmon, *Salmo salar*.

New DNA technology allows the measurement of genetic diversity in closely related groups over broad spatial and temporal scales. The power of genetic data rests in the consistent and large set of molecular characters that have been generated through evolution that retain unique temporal and spatial scales (functional genes, regulatory genes, proteins, repetitive DNA, etc.) We can analyze differences in genetic diversity across a species' range to identify physical or geologic patterns in the landscape that have influenced population structure over long periods of time. We can monitor the degree and scale of change in genetic diversity within dwindling populations and estimate extinction rates or persistence patterns. Stock transfers to novel environments, founder effects, and the effects of interbreeding among divergent populations can be monitored using DNA. We can follow patterns of paternity and investigate individual behavior over time without invasive sampling. Studies are beginning to

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J.L. Nielsen. Pacific Southwest Research Station, USDA Forest Service, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, U.S.A. e-mail: jnielsen@leland.stanford.edu

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identify patterns of genes or genetic characters within individuals that contribute to the extreme morphological and behavioral flexibility inherent in many species, both in higher vertebrates and the invertebrates. With time and effort, all of these methods and techniques are transferable to studies of fish and aquatic communities.

The magnitude of the recent growth in our knowledge of genetic structure, gene organization, and biochemical molecular processes, however, is paralleled with a clear understanding of how little we really know about the underlying principles of evolution and genetic mechanisms. Therein lies much of the controversy in today's field of population genetics. It is difficult to put a value scale on divergent interpretations based on competitive assumptions when the truth about the actual processes leading to evolution and changes in population structure over time are still in debate within the scientific community.

In this paper I will cover the general framework about what we know and do not know about patterns of evolution and molecular genetics markers in relation to investigations of fishes, especially salmonids and the Atlantic salmon. I will discuss issues of conservation and restoration in relationship to the new tools available from molecular population genetics and provide reference to numerous case studies recently published involving molecular genetics and Atlantic salmon.

Population structure and evolution in fishes

In the study of molecular population genetics it is impossible to extract our understanding of the organism from our knowledge of the molecular process. Populations are made up of individuals, and individuals are thought to form the basic component of natural selection in most vertebrate species. The fundamental principles of heredity discovered by Gregor Mendel in the 19th century demonstrated how individual traits are inherited from parent to offspring. Simple, independent transmission of genetic characters across generations remains the underlying assumption in most genetic studies of population structure. The concept that genetic traits can be traced back through generation after generation to reach a common ancestor is the foundation of the study of phylogeny and evolutionary history (Avise 1994).

Genetic diversity within a population can result from two primary processes: natural selection for adaptive traits and genetic drift (stochastic shifts in genetic signatures over time that are thought to be neutral in relation to natural selection). Most adaptive characteristics recognizable at the organism level are thought to be the product of multiple gene complexes and not the result of single gene mutations or simple DNA changes. Our understanding of the biochemical interactions and feedback loops involved in characterizing complex character states are still in their infancy, even in our intensive study of the human genome. Clearly, the next 20 years will bring significant insight into these complex genetic interactions that will provide new tools for our understanding of population substructure based on natural selection.

The evolution of genetic diversity within any given population is clearly driven by internal biochemical forces that are subject to selection at the organism level, but population genetic diversity is equally subject to the functional constraints of replication and gene expression (Maizels and Zimmer 1991). Recent invertebrate studies suggest that nutritionally influenced developmental plasticity based on the level of expression of regulatory genes, not changes in gene structure, may be a involved in extreme morphological and behavioral specialization associated with certain social insects (D. Wheeler, Univ. AZ, Tucson, personal communication) This may also be the case for the diversity of ecomorphs found in various fish species flocks. Identification and explanation of the molecular processes thought to influence patterns of genetic diversity subject to natural selection remain fundamental problems in evolution and conservation (see Hard 1995).

Typically, the molecular markers used in defining population structure (both protein and DNA) are thought to be neutral (or nearly so) in relation to selection (Ohta 1997; Zuckerkandl 1997). These markers show no direct association or linkage to known selective processes at either the organism or the molecular level. Changes in these molecular markers are thought to result from genetic drift and (or) migration of individuals among population subgroups. Studies based on "tiny bits of DNA" are often criticized as incoherent and having little or no relevance to speciation or evolution. It is important, however, to remember that many relevant heritable characters (including some physiological traits) have been shown to have their basis in only slight changes of DNA. One case to consider is the large number of heritable human diseases that are linked to simple changes in the number of nucleotide repeats found at individual microsatellite loci in the human genome (Caskey et al. 1992; Karlin and Burge 1996). Arguments continue over the selective neutrality of different molecular characters in common use today (Kimura 1983; Eanes 1987; Ballard and Kreitman 1995; Powers and Schulte 1996).

One advantage of the new DNA-based molecular techniques is the consistent and large set of characters that are currently available for comparisons of DNA derived from contemporary samples and older collections of dried tissue and (or) scales (J.L. Nielsen 1996; E.E. Nielsen et al. 1997; J.L. Nielsen et al. 1997*b*). To support evidence of genetic associations within and between closely related populations and trace them over short periods of time is not all that easy, however. Theory and mathematical simulations have provided guidelines and models (sometimes conflicting), such as the "infinite allele" and the "stepwise" mutation models, for new molecular markers (Roff and Bentzen 1989; Shriver et al. 1993; Valdes et al. 1993; Goldstein et al. 1995; Slatkin 1995; Takezaki and Nei 1996).

There is currently no consensus on their use when applied directly to empirical studies (see J.L. Nielsen et al. 1997*a*). We know from recent empirical studies that the molecular basis or mode of change and transmission in selectively neutral markers can be highly variable in different genetic systems (Nei 1987; Birky et al. 1989; Brooker et al. 1994; Lee et al. 1995). In any population study, clear knowledge and explanation of the assumptions imposed by our interpretation of patterns of variation found using different genetic models and (or) different parts of the genome are very important.

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While organismal studies using morphological characteristics have been very successful in defining relationships at the level of the genera or species, molecular studies have been most successful at interpreting relationships at lower taxonomic scales, either among populations or for the interpretation of intraspecific biogeographic structure. Empirical studies at the lower systematic levels have been providing insight over the last decade into the mechanisms by which the extensive diversity of fish population structure has evolved (Ryman 1983; Guyomard and Krieg 1983; Fergusson 1989; Bernatchez et al. 1992; Utter 1994; Phillips et al. 1994; Utter et al. 1993; Wenburg et al. 1996; J.L. Nielsen et al. 1997*a*; Stepien and Kocher 1997 and literature therein). Recent developments of new molecular DNA markers have contributed significantly to this issue.

Microsatellite DNA loci – highly repetitive tandem repeats of specific DNA sequence (Hughes and Queller 1993), have recently been widely used to analyze parentage, mating systems, and cryptic population structure in closely related groups of animals (Queller et al. 1993; Bowcock et al. 1994; J.L. Nielsen et al. 1994*a*; Angers et al. 1995; McConnell et al. 1995*a*; O'Reilly and Wright 1995; Quinn et al. 1996; O'Reilly et al. 1996). The high level of polymorphism observed at microsatellite loci suggest accelerated mutation rates (10^{-2} to 10^{-5}; Weber and Wong 1993) compared to either allozymes or mitochondrial DNA. Such variation would suggest that population differentiation using microsatellites would be more sensitive to changes resulting from population breeding size, dispersal rate, and population substructure over recent history. The mutational mechanisms underlying the highly polymorphic allelic structure found in most microsatellite loci, however, remain controversial (Di Rienzo et al. 1994; Pemberton et al. 1995; Garza et al. 1995; Jarne and Lagoda 1996).

Conservation and restoration issues

Fine-scale molecular studies are providing the foundation upon which management decisions and conservation guidelines are developed for many fish species. "Evolutionarily Significant Units" (ESUs) and other genetically based management units for fisheries are quickly making their way into conservation and policy decisions throughout the U.S. (Waples et al. 1990; Hedrick and Miller 1992; Utter et al. 1993; J.L. Nielsen 1995, 1996*a*; Waples 1995). Recent fisheries conservation issues addressed by analyses of molecular genetics have included: temporal changes in allele frequency (Waples 1989; Brown et al. 1996; Hansen and Mensberg 1996; Richards and Leberg 1996; E.E. Nielsen et al. 1997); gene diversity vs. biodiversity (Milligan et al. 1994; Lande 1995); endangered species, captive broodstock development, and the estimation of effective population size (Hedrick et al. 1994; Waples and Do 1994; Allendorf and Waples 1996; Banks et al. 1996; Tessier et al. 1997); problems of inbreeding between hatchery and wild stocks (Hindar et al. 1991; Waples 1991; J.L. Nielsen et al. 1994*b*; Ryman 1994; Tessier et al. 1995; McConnell et al. 1995*b*; J.L. Nielsen 1996*a*,*b*); metapopulation structure in fishes (Mayden and Wood 1995; Fontaine et al. 1997); the effects of wild stock transfers in relic populations (DeMarais et al. 1993; Quinn et al. 1996; J.L. Nielsen et al. 1997*b*); and inbreeding and outbreeding depression in wild fish stocks (Frankham 1995; Allendorf and Waples 1996). All of these studies have important implication for the management and conservation of Atlantic salmon across temporal and spatial scales.

Case studies in population genetics — Atlantic salmon

Atlantic salmon are a highly migratory species with complex life history patterns demonstrating significant local adaptation (Taylor 1991), homing behavior during reproduction (Sabell 1984), and a complex suite of reproductive strategies (Fleming 1996). Questions of life history structure and the influence straying and homing would have on an anadromous species have led to speculation about the application of the metapopulation concept to this group of organisms (Power 1981). Genetic population structure of Atlantic salmon, with differentiation of broad geographic stocks has been discussed in the literature for over two decades (Saunders and Bailey 1978). Three major genetic discontinuities have been demonstrated in members of this species from the North Atlantic, the western Atlantic, and the Baltic sea (Ståhl 1987; Davidson et al. 1989; Altukhov and Salmenkova 1991; Jordan et al. 1992). A brief overview of the more recent literature provides insight into the way these questions have evolved.

As early as 1982, allozyme studies were used to document genetic differentiation among natural stocks of Atlantic salmon from the northeast Atlantic (Ståhl 1982; Koljonen 1989). Verspoor et al. (1991) found significant heterogeneity for protein allelic variation among Atlantic salmon stocks from tributaries in the Kyles of Sutherland river system in northeast Scotland. A third study of genetic variation within a single catchment in southwest England revealed significant differences for one protein locus among stocks in three tributaries (Hurrell and Price 1993). Allozyme studies have tested the feasibility of using genetic stock identification to analyze seasonal changes in stock contribution in different fishing zones (Koljonen and McKinnell 1996). This study showed that the proportion of catch from two stocks could be separated independently, but the remaining groups tested were thought to contain a composite of four different stocks with low genetic identification predictability.

Mitochondrial DNA (mtDNA) studies have also shown significant differences in genetic structure among geographically proximate populations of Atlantic salmon (Bermingham et al. 1991; King et al. 1993; Moran et al. 1994; Tessier et al. 1995; E.E. Nielsen et al. 1996; Tessier et al. 1997). Taggart et al. (1995) were able to discriminate between European and North American Atlantic salmon using a minisatellite marker. More recently, nuclear microsatellite markers have been used to identify and test hypotheses of genetic population structure in Atlantic salmon in both Europe and Canada (McConnell et al. 1995*a*,*b*; O'Rielly et al. 1996; Fontaine et al. 1997; Tessier et al. 1997).

In studies using more than one class of molecular marker (Tessier et al. 1995; Verspoor et al. 1995; Tessier et al. 1997), the most powerful discriminating markers were found to be nuclear microsatellite loci. Rigor of results in these comparative studies differed between mtDNA and allozymes, depending on the type of markers used for each class. Biogeographic population studies done so far on Atlantic salmon stocks support significant allelic heterogeneity

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among rivers, suggesting that each riverine population should be considered a separate management unit and not as part of a broader metapopulation (Fontaine et al. 1997).

Genetic discrimination of within-river stocks with unique temporal migration patterns in Pacific salmon are well documented (J.L. Nielsen et al. 1994*c*; J.L. Nielsen 1996*a*; Banks et al. 1996). These studies, using mtDNA and microsatellites, give some insight into anadromous metapopulation structure within individual rivers. Several studies have tested the hypothesis of within-stock genetic diversity for different life history adaptations in Atlantic salmon, primarily between co-occurring anadromous and non-anadromous morphs (Ridell et al. 1981; Verspoor 1986; Palva et al. 1989; Verspoor and Jordan 1989; Birt et al. 1991; Jordan et al. 1992). All of these studies supported the inference of genetically distinct sympatric populations of anadromous and non-anadromous Atlantic salmon.

Investigations into direct links between genetic markers and known adaptive characters are more rare for Atlantic salmon. Verspoor and Jordan (1989) were able to demonstrate that changes in the locus encoding malic acid (Me-2) in Atlantic salmon were distributed according to temperature conditions experienced by local endemic stocks. Nathanailides and Stickland (1996) studied fast growing vs. slow growing salmon for differences in enzyme activity (cytochrome *c* oxidase and lactate dehydrogenase). Their study indicated a higher aerobic/anaerobic metabolic potential in the fast growing fish. Further research on within-population genetic diversity linked to selective characters is clearly needed (Power and Power 1987; Robitaille et al. 1986; Verspoor 1994).

Genetic effects of hatchery or farm propagation of Atlantic salmon has been an issue for the last decade (Cross and King 1983). The impact of hatchery/farmed supplementation on the integrity of wild populations has also received significant study in the Atlantic salmon (Gausen and Moen 1991; Jonsson et al. 1991; Einum and Fleming 1997). On October 1, 1996, the New York Times reported that Norwegian researches have discovered that more than 25% of the spawning Atlantic salmon in Norwegian waters are escapees from farm fish. With their classic study, Hindar et al. (1991) initiated a discussion over how changes in homing behavior and unique life history characteristics in Atlantic salmon occur following artificial culture producing significant genetic (and potentially adaptive) impacts on the locally adapted wild stocks. Other studies have supported their hypothesis by showing significant genetic changes in cultured fish (Knox and Verspoor 1991; Youngson et al. 1991; Crozier 1993) and provide speculation on the threats these changes may have on endemic wild stocks (Bentsen 1994; Tessier et al. 1995, 1997).

Transplantation of species and stocks across ecological barriers has been a widespread activity in both fish farming and cultivation of Atlantic salmon (Kazakov and Titov 1993; Bentsen 1994). Changes (usually loss) in genetic diversity within populations of Atlantic salmon derived from the admixture of hatchery (farmed) and wild fish appears to happen within only one generation (Verspoor 1988; Koljonen 1989; Gjedrem et al. 1991; Mork 1991; Tessier et al. 1997). These changes are probably due to a reduction in the effective breeding size and (or) selection for phenotypic characteristics during propagation (Ryman and Laikre 1991; Ryman et al. 1995). Most studies have demonstrated continuous gene flow both ways between farmed/cultivated stocks and wild populations, with a subsequent loss of genetic diversity in the wild spawning groups (Ryman and Laikre 1991; Elo 1993; Tessier et al. 1997). Unpublished results from a study of the genetic population structure of the Atlantic salmon used for restoration in the Connecticut River over the last 20 years show that the number of microsatellite alleles is reduced in the hatchery stock by 25% when compared to the wild donor stocks (B.H. Letcher, Conte Anadromous Fish Research Center, Turner Falls, Mass., personal communications).

These findings suggest that in forming artificial populations for supplementation or cultivation, the intrapopulation genetic diversity of Atlantic salmon has often not been taken into account, creating significant complications in our efforts to conserve wild endemic stocks (Ryman et al. 1995). They also suggest that to preserve the genetic diversity within artificially propagated populations of salmon, a return to the diversity of genetic material available from local wild populations will continue to be necessary. Genetic perturbations caused by supportive breeding programs can, however, be reduced by improving supplementation practices and taking population genetic factors into account (Tessier et al. 1997).

Conclusions

The published literature suggests that significant subdivisions have been found in the population genetics of Atlantic salmon over broad geographic regions (North Atlantic, the western Atlantic, and the Baltic sea); among tributaries within individual river basins throughout Europe and Canada; and between sympatric phenotypes within specific rivers. A knowledge of the biological, behavioral, and evolutionary forces that dictate the zoogeographic distribution of *Salmo salar* genotypes throughout the eastern and western Atlantic Ocean have only been speculated on. The issue of local adaptation and differentiation of gene structure among geographically distinct lineages based on neutral and not-so-neutral genetic markers needs to be explored further across the full extent of the range of the species. Considerations of evolutionarily significant units (ESUs) for the conservation of this species seem especially important to the issues of stock transfers, supplementation, and artificial propagation that remain an integral part of the ongoing management of this species.

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Interactions between wild and introduced Atlantic salmon (*Salmo salar*)

A.F. Youngson and E. Verspoor

Abstract: Wide latitude exists for genetic, behavioural, and ecological interactions between introduced and wild Atlantic salmon (*Salmo salar* L.). These can occur at all stages of the life cycle and across the range of natural environments the species exploits. Because of the large number of variables and scales involved, each interaction scenario and its outcome is expected to be unique. However, as a general rule, interactions are likely to be negative in their effect on the viability of wild populations. In theory, it ought to be possible to develop approaches for managing interactions, but in the particular case of genetic effects this is especially difficult. It is possible to put forward two guiding genetic principals for intentional introductions. Firstly, when introductions are used to maximize local abundance, genotypic diversity must be maintained so that mean individual fitness remains undiminished after interaction has occurred. Secondly, when introductions are used to alter local frequencies of phenotypes, the population's capacity to remain viable in the longterm must not be impaired. Both principals are pragmatic and aim to conserve or restore the genetic capacity of populations to evolve rather than seeking the preservation of their current condition.

Résumé : Il existe d'importantes possibilités d'interactions génétiques, comportementales et écologiques entre les saumons atlantiques introduits et sauvages. Ces interactions peuvent se produire à tous les stades du cycle vital et dans l'ensemble des milieux naturels exploités par l'espèce. En raison du grand nombre de variables et d'échelles en jeu, on doit s'attendre à ce que chaque scénario d'interaction et ses résultats soient uniques. Cependant, en règle générale, les interactions ont probablement des effets négatifs sur la viabilité des populations sauvages. En théorie, il devrait être possible d'élaborer des méthodes de gestion des interactions, mais cela serait particulièrement difficile dans le cas précis des effets génétiques. On peut établir deux principes directeurs sur le plan génétique aux fins des introductions intentionnelles. Premièrement, quand les introductions sont utilisées pour maximiser l'abondance locale, la diversité génétique doit être maintenue de façon à ce que la valeur adaptative individuelle moyenne ne diminue pas après l'interaction. Deuxièmement, quand les introductions de poissons d'élevage sont utilisées pour modifier les fréquences locales des phénotypes, la capacité de la population de demeurer viable à long terme ne doit pas être diminuée. Ces deux principes sont pragmatiques et visent à conserver ou à rétablir la capacité génétique des populations d'évoluer et non pas seulement de demeurer dans l'état où elles se trouvent.

[Traduit par la Rédaction]

Background

Introductions of Atlantic salmon (*Salmo salar* L.) have been carried out since the mid-19th century when methods were first developed for stripping adult fish, and rearing eggs and fry in hatcheries. Over the last two or three decades, more sophisticated techniques have been used over much of the natural range of the species to drive large-scale enhancement schemes involving introductions of fry, parr, or smolts (see e.g., Meyers 1995; Moring et al. 1995) and to sustain commercial aquaculture. The development of aquaculture has led to the presence of all life stages of escaped farmed salmon in the wild, across much of the species' natural range. As a result of both intentional and inadvertent releases, introduced salmon are now widespread and often frequent among naturally spawned fish in rivers (Lund et al. 1991; Webb et al. 1991; Webb and Youngson 1992; Webb et al. 1993) and in the sea (Hansen et al. 1993, 1997). Accordingly, wide latitude exists for genetic, behavioural, and ecological interactions between wild and introduced fish at all stages of the life cycle and across much of the range of natural environments that salmon exploit.

In general terms, the outcome of interactions between introduced and wild fish will be mediated by:

(1) the viability of introduced fish in their new social and physical environments;
(2) the capacity of introduced fish to exert direct effects on the fitness of competing wild fish;
(3) the capacity of introduced fish to exert indirect effects on the fitness of wild fish, for example, through disease transfer;
(4) the reproductive fitness of introduced fish relative to wild fish.

The least interventionist forms of introduction for enhancement are made by moving sexually mature adult salmon (Thomas 1996; Kapuschinski 1997) or naturally spawned progeny among locations. Interactions from these practices are least likely to be problematic. Problems are more likely to occur in relation to introductions of fish that have been subject to hatchery rearing (including commercial

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A.F. Youngson. FRS Freshwater Fisheries Laboratory, Faskally, Pitlochry, Perthshire, U.K.
E. Verspoor. FRS Marine Laboratory, Aberdeen, U.K.

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aquaculture) for at least a part of their life cycle and for one or more generations. In situations like these, the viability of introduced hatchery fish will be determined by:

(1) the genetic characteristics of the source population for the introduced salmon;
(2) the extent of any deliberate or inadvertent genetic selection at the parental or prior generations;
(3) the quality of the environment in which the introduced fish are reared;
(4) how much of their life cycle is spent in culture;
(5) the quality of the natural environment to which they are introduced;
(6) the qualities of their wild competitors.

Each of these factors is determined by a complex interaction of variables. Each factor is influenced by considerations related to the numerical, spatial, and temporal scales under which they occur. Thus, at the most local scale, the spatial dimensions of introductions will determine the effective density of the introduced fish and the extent to which they finally interbreed among themselves or with wild fish. At larger geographical scales, the origins of introduced fish relative to the receiving wild population will often determine the extent of genetic differentiation between the two groups (Verspoor 1997). Temporal scales may range from effects on viability measured in terms of weeks or days (e.g., introductions at critical life-history stages (Larsson 1977)) or even hours (introductions made by day or at night (Hansen and Jonsson 1986)), to those at the decadal or generational timescales that are appropriate, for example, to considerations of climatic change or natural selection. When all the relevant scales are taken into account the extreme difficulty in predicting (or even describing) the outcome of interactions becomes apparent. Because of the large number of variables and scales involved, it is also evident that each interaction scenario and its outcome is likely to be unique.

All the factors driving interactions can be placed into either of two broad categories — differences between natural and hatchery environments, and differences between the genetic make-ups of wild and introduced fish. A substantial literature indicates that both groups of factors are potentially important. Although some of the most relevant information refers specifically to salmonids other than Atlantic salmon, much of it can probably be validly generalized. On this basis, three main issues are examined below — the separate effects of environmental and genetic factors in determining the relative viability of introduced and wild fish, and the effects of introduced fish on the character of stream populations.

Environmental effects

Environmental effects on the viability of introduced salmon

The environments to which fish are exposed in hatcheries are highly atypical of all wild environments. The physical character (e.g., flow, temperature regime), and the intraspecific (social) and interspecific (e.g., diseases and parasites) aspects of natural and hatchery environments all differ. Prior responses to the hatchery environment will affect the capacity of released fish to become established in the natural environment by inducing physiological or behavioural modification. These responses may be to physical environmental parameters (Hosmer et al. 1979) or rearing density (Ewing and Ewing 1995) and include first-generation changes in aggression (Siikavuopio et al. 1996). Similar effects, in some cases attributed to domestication, are reported for aggressive behaviours (Berejikian et al. 1996; Einum and Fleming 1997), predator avoidance (Berejikian 1995; Johnsson et al. 1996), life-history traits (Finstad and Heggberget 1993; Johnsson et al. 1993, 1996; Petersson et al. 1996), fecundity (Jonsson et al. 1996), and morphology (Fleming et al. 1994; Petersson and Järvi 1997). Even in low intervention procedures (e.g., stocking of unfed fry derived from wild parents) changes due to the physical environment of hatcheries are possible (Nathanailides et al. 1995). All these effects, many of which are likely to be interlinked, are potential effects on the ability of reared fish to survive and to interact with wild fish after release.

The availability of potential territories for salmon in streams is space-limited and competitively determined (Grant and Kramer 1990). For introduced fish, there will be an immediate requirement to obtain resources (space, food, and shelter) in competition with non-naive, wild conspecifics with established territories. In general, the effects of hatchery rearing on the viability of introduced fish in a competitive natural environment are expected to be negative. However, case-specific exceptions may occur — in relation to size as it effects dominance, for example (Berejikian et al. 1996). For wild fish, the availability of resources, the command of resources by individuals and the development of the group are expected to be in some form of equilibrium (Gibson 1978; Gibson and Dickson 1984; Chadwick 1987, 1993; Marschall and Crowder 1995). Rearing regimes free the development of hatchery fish from natural environmental constraints imposed through growth and, in general, development is accelerated (Thorpe 1991). This is expected to lead to mismatches between the requirements of released fish and the structure of the resources potentially available to them. In addition, the seasonal structure of the physical environment is a determinant of the viability of released fish. For example, post-release survival of cultured smolts varies with release date and survival is grossly impaired outside a brief time-window in spring (Larsson 1977; Hansen and Jonsson 1989; Staurnes et al. 1993).

Modification of the natural environment by introduced salmon

Introduced fish alter the natural stream environment of wild salmon by elevating densities and increasing overall levels of competition, in some cases to the disadvantage of indigenous fish (Einum and Fleming 1997; McGinity et al. 1997). Introductions can also lead to predator attraction, by raising local fish densities or because of aberrant forms of behaviour, and this may also result in increased mortality among wild fish (Hvidsten and Lund 1988). Introduced fish sometimes modify natural environments through the introduction of parasites or disease organisms. Notable examples of this effect include the introductions of the monogenean parasite, *Gyrodactylus salaris* (Johnsen and Jensen 1991) and the bacterium, *Aeromonas salmonicida* (Håstein and Lindstad 1991) to Norwegian waters. In both cases, the first appearance of the organisms in Norway has been linked to the introduction of salmon from other regions. In both cases,

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the introduction of the pathogens has resulted in high levels of mortality among wild Norwegian salmon. In the case of *Aeromonas salmonicida*, immunization is an effective control measure for cultured fish but, in spite of treatment, some escaped aquaculture fish remain *Aeromonas* carriers (Hiney et al. 1997).

Genetic effects

Genetic effects on the viability of introduced salmon

Mortality rates in hatchery environments are lower at all stages than those that pertain in the natural environment. Scope for selective mortality among phenotypes is therefore reduced. When selection does occur it is in response to novel selective pressures. These may be applied deliberately, through brood stock choice for genetic improvement of farmed strains of salmon, or inadvertently as a result of sampling bias. In commercial aquaculture, deliberate genetic selection has been applied in breeding schemes based on individual and family selection — notably in Norway (Gjedrem et al. 1988), Canada (Friars et al. 1996), and Iceland (Jonasson 1996) — in successful attempts to alter the distribution of phenotypes among farmed fish. Elsewhere, the intuitive use of informal protocols directed towards the same ends has been widespread. Fleming and Einum (1997) reported that the morphology, growth, and behaviour of juvenile salmon tested in a simulated stream environment, differed between a cultured strain and its wild source population after several generations of selection. The most extreme type of phenotype manipulation involves the construction of new genotypes using genetic material derived from other species (Hew et al. 1995). On release or escape to the wild, extreme phenotypic development of hatchery fish is again likely to lead to mismatches with available natural resources. If genetically selected fish prove capable of successful reproduction, similar mismatches will be propagated in following generations of the local population, through altered gene frequencies and the increased prevalence of phenotypes that were previously absent or infrequent.

Hatchery effects on reproductive fitness

Lifetime performance of introduced salmonids relative to wild fish has been examined in a number of field studies that have used physical tags or allozyme markers to distinguish wild and introduced fish (Bams 1976; Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Mayama et al. 1989; Leider et al. 1990; Chilcote et al. 1991; Crozier 1993). In general, these studies indicate that lifetime fitness is reduced in introduced fish. Experimental studies suggest that the reproductive behaviour and reproductive performance of hatchery-reared fish of both sexes is impaired, especially in competition with wild fish (Fleming and Gross 1992; Fleming et al. 1996; Petersson and Järvi 1997). Impairment has been attributed to domestication and, among farmed salmon, may be coupled with deliberate selection for production traits. Reduced lifetime fitness will lower the ability of introduced fish to generate interactive genetic effects in wild populations. However, some residual effect is expected since the spawning of escaped farmed salmon among wild fish is widespread and sometimes common (Lura and Sægrov 1991; Webb et al. 1993). Skaala et al. (1996) demonstrated that reproductive performance in introduced *Salmo trutta* is impaired relative to wild fish. In addition, they showed that the relative survival of the progeny of introduced fish was progressively reduced over time relative to non-hybrid progeny. In general, the findings of studies like these cannot be attributed specifically to the effects of introduction rather than to the effects of culture, since non-interactive genetic or environmental effects, including maternal effects, may be involved in each case.

Effects of introduced salmon on the character of wild populations

Post-reproductive genetic effects

In a recent review, Verspoor (1997) has argued that wild populations of Atlantic salmon are genetically heterogeneous for single- and multi-locus traits, within and among catchments across the species' range. However, the adaptive importance of these effects and the extent to which the performance of wild populations of salmon is likely to be altered by interbreeding with introduced fish is poorly understood. Studies of genetic variation at enzyme loci have demonstrated widespread differences between the genetic make-ups of hatchery lines of salmon and the wild founding stocks from which they have been derived (Cross and King 1983; Ståhl 1983; Verspoor 1988; Crozier and Moffett 1989; Koljonen 1989; Cross and Challanain 1991; Youngson et al. 1991). It is usually assumed, however, that enzyme variation is neutral with respect to performance and therefore that any changes in allele or genotype frequencies following the introduction of reared fish are likely to be without effect on the performance of the recipient population.

On the other hand, the assumption of neutrality does not appear to be operationally valid for a number of enzyme polymorphisms for which geographical or performance correlates have been detected (Verspoor and Jordan 1989; Torrissen 1987; Pollard et al. 1994). The most striking of these exceptions is the *MEP-2** locus. Among wild populations of Atlantic salmon, the frequency of the alternative *MEP-2** alleles is correlated with environmental temperature, among and within catchments (Verspoor and Jordan 1989; Verspoor et al. 1991). In addition, growth (Jordan and Youngson 1991) and sea-age at sexual maturity (Jordan et al. 1990) differ among *MEP-2** genotypes. This general picture suggests that *MEP-2** variation (or, perhaps, linked variation in a more extensive gene complex) is of local, adaptive significance (Jordan et al. 1997). In cases like these, changes in allele and genotypes frequencies are expected to be a potential effect of introductions on the performance of populations.

For Pacific salmon, the assumption that local genetic adaptation exists, and the belief that it is noteworthy and biologically and economically important, has made the maintenance of genetic population structuring a major driving theme in management (see e.g., National Research Council 1996). However, in Europe and eastern North America, population structure and local adaptation have been adopted more slowly as management themes for Atlantic salmon and are not universally acknowledged (see e.g., Bentsen 1991). A large body of mostly circumstantial

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evidence for local adaptation with respect to complex, multigenic traits has been reviewed in the context of Atlantic salmon by Saunders (1981), Taylor (1991), Hindar et al. (1991), and Verspoor (1997).

For Atlantic salmon, the most direct evidence for local adaptation relates to the resistance of the populations of the Baltic rivers to the parasite *Gyrodactylus salaris*. Salmon from non-Baltic populations (which have no history of exposure to the parasite) show little or no resistance to its effects, which are usually lethal (Bakke et al. 1990; Bakke 1991). For salmonids generally, less compelling experimental evidence for adaptive genetic variation exists for many other aspects of performance. Effects are reported for body morphology (Riddell et al. 1981), seasonal run-timing in adults (Hansen and Jonsson 1991), growth capacity (Conover 1990; Nicieza et al. 1994), homing (Bams 1976; McIsaac and Quinn 1988), habitat preference (Hesthagen et al. 1995), timing of smolt migration (Orciari and Leonard 1996), and disease resistance (Beacham and Evelyn 1992; Fjålestad et al. 1993, 1996). In addition, variation is observed in the distribution of phenotypes for adult size (Schaffer and Elson 1975; Jonsson et al. 1991), run-timing (Saunders 1967; Laughton and Smith 1992), spawning time (Heggberget 1988; Webb and McLay 1996) and for age-at-maturity (Hutchings 1998). These observations have been used to develop hypotheses on local genetic adaptation but the genetic basis for the variations and their adaptive relevance have not been rigorously tested.

Scales of effect

All introductions — even those based on the least interventionist protocols — have the potential to disrupt local population structure. Many Atlantic salmon home with substantial accuracy at subcatchment scales before they spawn (Youngson et al. 1994). Reproductive isolation is sufficient to maintain heterogeneity in frequencies for *MEP-2** and other allozymes, at sub-catchment levels (Verspoor et al. 1991; Heggberget et al. 1986; Ståhl 1987; McElligot and Cross 1991; Jordan et al. 1992). Phenotype distributions for the fitness-related traits discussed above are also commonly observed to be heterogeneous on similar local scales. On this basis — even for first-generation hatchery groups intended to be returned to the same rivers — the effects of stock movement, non-random sampling, forced matings, and facile mating systems are all potential distorting effects on natural population structure. On the finest scale, the local overrepresentation of single hatchery families has the potential to distort populations that receive stocked fish (Ryman 1991).

Discussion

The single objective of most intentional introductions of salmon is to increase smolt production beyond natural levels. In most cases, unintended interactions between introduced and wild fish are inevitable because of the large number of possible effects cited above. While many of these effects are intuitively obvious, the implications of interactions are often not considered by those making introductions and interactive effects are seldom those that are planned. On the other hand, the chosen source for introduced fish has been conditioned by genetic considerations in some introductions. Attempts have been made to match source and recipient populations to minimize genetic disturbance, or to introduce fish with particular characteristics. An example of the former is the choice of southern Canadian rivers before Icelandic rivers, as a source of stock for continuing restoration work on the Connecticut River (Orciari et al. 1994). An example of the latter is the reported introduction of fish from more than 17 rivers into the River Polly in western Scotland (see Jordan et al. 1992). Introductions of these kinds might be regarded as the most defined of all. In cases of the latter type, especially, the underlying intention for the interactions that will result is explicit.

In theory, the development of protocols for managing introductions and the interactions that result should be possible, based on an understanding of the principles involved. Non-genetic, behavioural or disease interactions are not likely to be the intended effects of any introductions. Some of these effects are likely to be temporary and most present problems for which solutions can be envisaged (e.g., suppression of domestication or disease transfer through improved hatchery environments). In contrast, genetic interactions appear to be an inevitable and potentially permanent consequence of most introductions and they pose special difficulties. The concept of genetic population structuring in salmonids is not recent (see e.g., Menzies 1938). However, the present resurgence of interest in the concept has generated a new emphasis on the consideration of genetic factors in conservation and management. Recently, this area has been examined in a number of contexts (see volumes edited by Hansen et al. 1991, Thomas and Mathisen 1993, Neilsen 1995, and Schramm and Piper 1995). The status of natural populations of salmon is now considered to be a determinant of their current performance in the particular sequence of habitats that they exploit and also a determinant of their future capacity to develop. These views lead to the proposition that natural population structuring is an asset that should be conserved, especially in the face of apparently contrary pressures caused by poorly conceived enhancement schemes or by accidental introductions (Gross 1998). On balance, the arguments favouring this view are strong enough to justify an approach to the management of natural salmon populations that is strongly conservative in tone.

In considering the application of these views to Atlantic salmon management, several outstanding issues remain to be considered, although none can be addressed specifically because of lack of knowledge. Firstly, there is no well-developed understanding of the route by which present-day populations have become structured with respect to the phenotypic variations that are of potential adaptive significance. The roles of genetic drift and natural selection, or habitat destruction, fishery pressure, and past introductions, for example, are unknown. Secondly, neither the current genetic status of particular salmon populations nor current levels of diversity among populations can be ranked on any scale relative to their previous conditions because these are, at best, poorly documented for a recent, brief period in the population's development. Thirdly, there can be no expectation for how genetic population structure might continue to evolve in the course of future events and therefore no specific indication on how to guide management. Thus, justification for exposing local populations to, or protecting them

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from, any form of management involving genetic interactions can be based only on a consideration of general biological principles.

At present, management of the genetic interactions that arise from introductions can be achieved only by managing the introductions themselves. In this regard, two guiding genetic principles can be identified. Firstly, where the objective of intentional introductions is to maximize local abundance, genotypic and phenotypic diversity should be conserved at the appropriate local scale so that mean individual fitness remains undiminished. Secondly, where the objective is to optimize local production (according to some management target) by altering genotype or phenotype frequencies, the population's capacity to evolve should not be impaired. In either case, the key to implementing such schemes is the ability to assess diversity or adaptive capacity. Both these conceptual areas (and especially the latter) require further development but every introduction ought to share the same objective — to achieve an informed and balanced effect on the complex of characters that defines populations. Current knowledge is insufficient to support informed introductions and all interactions — genetic, behavioural, and ecological — must therefore be regarded as belonging to a single, untargeted class. On these grounds, all introductions must be regarded as injudicious.

From a management point of view, this position will prove to be untenably negative. At one extreme, it might be used to justify inaction and the imperfect preservation of fragmentary relicts of natural populations. At the other extreme, a contrary approach is certain to be adopted by agencies or individuals who deem the risks of introductions — including escapes from aquaculture — and the consequences of interactions to be an acceptable side-effect of their activities. Based on current thought, neither of these extremes is likely to prove satisfactory in the longer term, on either biological or economic grounds. Both positions, however, point up the necessity of developing a greater (or more convincing) understanding of the population genetics of salmonids. Unfortunately, this is an area where developing theory has outstripped empirical (and intuitive) understanding of the functioning of natural systems.

Local genetic adaptation appears to be a key factor. The evidence for its existence and its importance is circumstantial and incomplete (Verspoor 1997) but sufficiently compelling to conclude that a precautionary approach to the management of introductions is essential. It is very unlikely that it will become possible to develop an exact, positive approach to the management of adaptation, based on a better-developed understanding of the phenomenon, because of its essentially dynamic and complex nature. However, there is an increasing likelihood of many salmon populations reaching a sub-optimal state of adaptation — including those, for example, that are being repeatedly affected by the spawning of large numbers of escaped farmed fish. Given the scale of these events, it is correspondingly likely that genetic management based on intentional introductions will be attempted in future.

Although the precautionary principle would indicate that there should be a strong presumption against introductions, there is also a need for a rationale for carrying out introductions where the weight of scientific evidence suggests they are necessary. Such a rationale would emphasise the facilitation of the process of microevolution rather than the achievement of its results (local adaptation), using a development of the two guiding genetic principles identified above. Thus, an additional objective for management might be added to those that seek to restore abundance to historical levels or to conserve or restore the distribution of phenotypic variations among local populations. By raising genotypic diversity, future enhancement effort might target the capacity of populations to self-optimize in response to the series of environments they exploit during the course of a complex life cycle. This approach to management would emphasise the future genetic capacity of populations, rather than their past performance or their current condition. However, extended assessments of current and historical distributions of genetic or phenotypic variations among populations might be used to provide guidance on the most appropriate type of intervention to make. Introductions will remain problematical in view of the high degree of uncertainty associated with their outcomes. Accordingly, gradual, small-scale approaches are indicated for which the consequences of errors are likely to be correspondingly slight and from which small benefits will accrue incrementally. Equally, an experimental approach is essential where feedback is obtained from monitoring, and guidance is generated within a framework of adaptive management (see e.g., Kapuscinski 1997).

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Atlantic salmon (*Salmo salar*) in winter: "the season of parr discontent[1]"?[2]

R.A. Cunjak, T.D. Prowse, and D.L. Parrish

Abstract: Winter is a dynamic period. Effects of the winter regime on northern streams and rivers is extremely variable and characterized by dramatic alterations in physical habitat to which Atlantic salmon (*Salmo salar*) must acclimate and adapt to survive. In this paper, we synthesize recent advances in the biological and hydrologic/geomorphic disciplines, with specific reference to Atlantic salmon overwintering in the freshwater portions of those running waters subject to freezing water temperatures. The specific requirements and adaptations for surviving winter at the three distinct life-stages in freshwater (egg, parr, kelt) are identified in relation to the characteristics of three biophysical phases: early winter (temperature decline and freeze-up), midwinter (ice growth and habitat reduction), and the break-up/warming phase. In a case study of Catamaran Brook (New Brunswick), a hydro-ecological analysis was used to explain interannual variability in juvenile abundance, especially for young-of-the-year salmon. A strong relation was found between winter discharge and interstage survival (egg to 0+, 0+ to 1+, 1+ to 2+) in 5 of 6 years. That is, juvenile salmon abundance in summer was highest following winters with high streamflow, presumably a function of habitat availability, especially beneath ice cover. However, the lowest measured egg-0+ survival (9.2%) was related to an atypical midwinter, dynamic ice break-up triggered by a rain-on-snow event that resulted in severe scouring of the stream-bed and redds. Thus, interannual variability in Atlantic salmon parr abundance from 1990 to 1996 was largely explained by density-independent (environmental) constraints to winter survival. The complexity of stream processes during winter underscores the need for interdisciplinary research to quantify biological change.

Résumé : L'hiver est une période dynamique. Les effets du régime hivernal sur les cours d'eau du Nord sont extrêmement variables et caractérisés par des altérations marquées de l'habitat auquel le saumon de l'Atlantique doit s'acclimater et s'adapter pour survivre. Dans cet article, nous faisons une synthèse des progrès récents en biologie et en hydrologie et géomorphologie, en traitant particulièrement du saumon atlantique qui hiverne dans les eaux douces de ces cours d'eau dont les températures approchent du point de congélation en hiver. Les exigences et les adaptations spécifiques pour la survie hivernale des trois stades dulcicoles distincts (oeuf, tacon, charognard) sont établies en rapport avec les caractéristiques de trois phases biophysiques : début de l'hiver (chute de la température et englacement), mi-hiver (croissance de la glace et réduction de l'habitat) et la phase de dégel et de réchauffement. Dans une étude de cas portant sur le ruisseau Catamaran (Nouveau-Brunswick), on a eu recours à une analyse hydro-écologique pour expliquer la variabilité interannuelle de l'abondance des juvéniles, particulièrement chez les jeunes saumons de l'année. On a observé une forte relation entre le débit hivernal et la survie interstades (oeuf à 0+, 0+ à 1+, 1+ à 2+) dans 5 années sur 6. Ainsi, l'abondance des saumons juvéniles en été était grande après les hivers caractérisés par des débits élevés, probablement parce que l'habitat disponible était plus important, particulièrement sous le couvert de glace. Cependant, on a observé le plus faible taux de survie du stade d'oeuf à l'âge 0+ (9,2 %) après un mi-hiver atypique caractérisé par une débâcle dynamique causée par la pluie, qui s'est soldée par un affouillement marqué du lit du cours d'eau et des nids de fraye. Ainsi, la variabilité interannuelle de l'abondance des tacons de saumon atlantique de 1990 à 1996 était largement tributaire de contraintes indépendantes de la densité (environnementales) pesant sur la survie hivernale. La complexité des processus fluviaux durant l'hiver fait qu'il est nécessaire de mener des recherches interdisciplinaires pour quantifier le changement biologique.

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R.A. Cunjak.[3] Department of Biology and Faculty of Forestry and Environmental Management, University of New Brunswick, Bag Service 45111, Fredericton, NB E3B 6E1, Canada.
T.D. Prowse. National Hydrology Research Centre, Environment Canada, 11 Innovation Blvd., Saskatoon, SK S7N 2X8, Canada.
D.L. Parrish. Vermont Cooperative Fish and Wildlife Research Unit,[4] School of Natural Resources, University of Vermont, Burlington, VT 05405, U.S.A.

[1]With sincere apologies to William Shakespeare.
[2]Contribution No. 41 of the Catamaran Brook Research Project.
[3]Author to whom all correspondence should be addressed. e-mail: cunjak@unb.ca
[4]The Unit is jointly supported by the Biological Resources Division/USGS, Vermont Department of Fish and Wildlife, University of Vermont, and the Wildlife Management Institute.

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Introduction

In the north temperate and subarctic latitudes which encompass the range of most Atlantic salmon, *Salmo salar* L., winter conditions last between 4 and 8 months, depending on geographical location. Freezing water temperatures, variable ice dynamics, snow accumulation, reduced solar radiation and photoperiod, pH depression, anoxia, ice surges, mechanical break-up events, flooding, and extremely low river flows are some of the characteristic physico-chemical conditions of the winter environment which confront cold-water species such as Atlantic salmon. In order to survive, stream fishes respond with a variety of tactics (Cunjak 1996) such as altering diel activity patterns, shifting microhabitats, moving variable distances to wintering areas, physiologically adapting to changing temperature and feeding regimes, and reducing energy expenditure to conserve depleted energy stores until replenishment in spring.

Much has been done in the past 15 years to elucidate the various physical processes occurring in winter in ice-covered rivers and to describe the dynamic nature of this season (e.g., Ashton 1986; Gray and Prowse 1993; Beltaos 1995). Similarly, many basic biological questions pertaining to overwintering by stream biota have been addressed (Ultsch 1989; Irons et al. 1993; Power et al. 1993; Cunjak 1996). However, an integrated treatment of physical winter conditions and concomitant ecological responses has generally been lacking (but see reviews by Prowse and Gridley 1993; Prowse 1994; Scrimgeour et al. 1994). The present paper synthesizes specific recent advances in the biological and hydrologic/geomorphic disciplines with respect to winter conditions in Atlantic salmon rivers. Given the unique habitat requirements and sensitivities inherent to the three freshwater stages of Atlantic salmon in winter (i.e., eggs, parr, and kelt), their biological responses were treated separately within distinct biophysical winter periods with an emphasis on implications for survival.

Winter, as referred to in this paper, is defined as that period immediately following egg deposition by Atlantic salmon (and coincident with a decline in water temperature) and extending until the loss of all surface ice (often accompanied by a major spate and snowmelt) or the commencement of smolt emigration. This biological definition is specific for the present subject (*S. salar*) and has been modified from one suggested by Cunjak (1996). The running waters reviewed in this paper are those subject to near freezing temperatures (<1°C) and, typically, ice-formation for some portion of the winter. Although some Atlantic salmon are known to rear in estuaries (Cunjak 1992; Kazakov et al. 1992) and lakes (Chadwick and Green 1985; Hutchings 1986; Kazakov et al. 1992; Erkinaro et al. 1995), this paper will limit its focus to lotic freshwater environments.

The paper has two objectives: first, to establish the concept of winter as a dynamic period (spatially and temporally) by identifying environmental conditions inherent to Atlantic salmon rivers in winter, and the specific requirements and adaptations for surviving winter at the egg, parr, and kelt stages. The second objective was to demonstrate the value of hydro-ecological analysis to explain density-independent (environmental) constraints to winter survival for a population of Atlantic salmon; this was accomplished by way of a case study.

Bio-physical phases of winter

Often thought of as a period of relative calm and inactivity, the winter regime of northern streams and rivers is actually a very dynamic period characterized by dramatic changes in physical habitat to which Atlantic salmon must acclimate and adapt. Many of the changes are due to the distinctive hydrologic regimes of cold regions that owe much of their uniqueness to the accumulation and ablation of snow and ice (Prowse 1990, 1994).

Although many processes are temporally interdependent, for ease of discussion, winter has been subdivided into three basic periods: early winter, midwinter, and break-up (often, but not exclusively a late winter event). Subsections review the major physical conditions that characterize each period, describe the varied biological conditions unique for distinct life-stages of Atlantic salmon, and discuss the implications of the most important biophysical relationships using specific examples from the literature.

Early winter

The early winter period in most northern rivers is characterized by general declines in solar input, air and water temperatures, and discharge — albeit with some intraseasonal variability introduced by, for example, late-autumn rainfall-runoff events. It can also be broken into two distinct phases: (*a*) the period immediately following spawning during which water temperatures decline from approximately 5°C to 0°C and (*b*) the subsequent period of first ice formation.

Cooling, water level decline, and photoperiod reduction

The hydrology of streams and rivers in cold regions is governed by a number of unique processes that control the timing, duration, and magnitude of flow and water levels. Consequently, hydrographs differ significantly from those characteristic of temperate climates (Prowse 1994). As winter approaches, less water is delivered by surface runoff to the main channel because of the accumulation of precipitation as snow. With the loss of flow originating from surface runoff, a steady recession begins in flow and water levels; the rate of decline being tempered primarily by additions of flow from groundwater and surface water bodies (e.g., ponds and lakes). Accompanying the decline in flow is a reduction in available fish habitat due to the drying of ephemeral low-order streams and the drying of margins of higher order streams.

The specific hydraulic conditions and substrate chosen by Atlantic salmon for spawning (Peterson 1978; Fleming 1996), in combination with the immobility of eggs, results in eggs having the most restrictive winter niche of all life-stages. The coarse (gravel/cobble) composition of the redds and their general occurrence in midstream locations at the downstream end (tail) of pools and runs has the advantage of providing a continuous recharge flow of water and oxygen to the eggs within the substrate. These hydraulic conditions are in marked contrast to those experienced in the redds of another common salmonid of eastern North America, the brook trout (*Salvelinus fontinalis*), which prefer to spawn in

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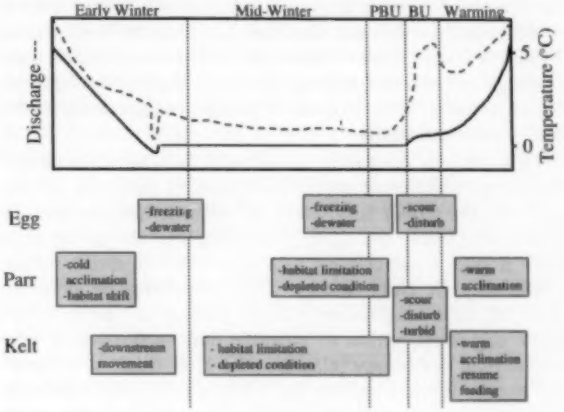
areas of "winter-warm" groundwater discharge (Curry and Noakes 1995), close to stream margins, and often with little regard for substrate particle size (e.g., Fraser 1982). The midstream location of salmon redds may be particularly adaptive because, as discharge and river stage decline (and border ice formation is subsequently initiated), streamflow becomes concentrated in the deeper portion of the channel (often midstream), thereby ensuring water delivery to eggs.

As water level and air temperature decline, water temperature also steadily falls (Fig. 1) although this is not a continuous process and is often interrupted by reversals in atmospheric heat fluxes. In general, the larger the surface area to volume ratio, the more efficient a river is in exchanging heat with the atmosphere. Hence, given the same meteorological conditions, wide shallow streams cool most rapidly while deeper rivers are usually the last to freeze. Inputs of groundwater also become increasingly important to the thermal balance as less surface runoff is directed to the stream. In many systems, including Arctic regions, "warm" groundwater is the main source of water that sustains winter streamflow (Reynolds 1997) and, where of sufficient magnitude, can keep sections ice-free. For some species, groundwater provides the only known overwintering and (or) spawning zones (Craig and Poulin 1975; Brown et al. 1994). Unlike many stream salmonids, Atlantic salmon (both wintering parr and spawning adults) appear *not* to seek out undiluted groundwater discharge zones in early winter (Cunjak 1996).

Coincident with a decline in daily water temperature below 8–10°C, juvenile Atlantic salmon display an autumnal shift in microhabitat choice and behaviour, moving beneath suitably sized stones during the daylight hours (Gibson 1966; Smirnov et al. 1976; Rimmer et al. 1983, 1984; Cunjak 1988*a*; Heggenes and Saltveit 1990; Veselov and Shustov 1991; Fraser et al. 1993; Erkinaro et al. 1995). Unlike the situation during summer when they are strongly photopositive (but see Gries et al. 1997), young Atlantic salmon become exclusively photonegative in winter (Rimmer and Paim 1990), leaving their shelters only during the night (or at dawn/dusk) to feed (Cunjak 1988*a*; Heggenes et al. 1993; Fraser et al. 1993). The reduced buoyancy of salmon parr at water temperatures <8°C (Pinder and Eales 1969) may be a synchronous adaptation for this cryptic behaviour. Frequency of emergence and nocturnal foraging is unknown, especially in far northern regions that are subject to months of polar darkness. Probably, foraging activity is minimal at such low temperatures because of the reduced metabolic demand and the inability to hold position in moderate water velocities (Rimmer et al. 1985; Heggenes and Traaen 1988) although visual acuity is improved at low light levels in winter (Fraser et al. 1993). Veselov and Shustov (1991) have suggested that this inability to resist water currents and the reduced fright reaction of overwintering salmon parr may explain the winter hiding behaviour — i.e., a tactic to avoid predation and minimize energy expenditure (Cunjak 1996).

There are, however, exceptions to the above-noted generalizations. At the northern end of their distributional range, such as in subarctic rivers (e.g., Ungava, Labrador, northern Scandinavia, and Russia), some young Atlantic salmon remain day-active above the substrate until water temperatures decrease below approximately 5°C (Cunjak, unpublished data). Such a variation seems adaptive where the growing season is so short because of the cold climate (Jensen and Johnsen 1986). Even in more temperate latitude streams such as in New Brunswick, juvenile salmon (age 0+ and 1+) have been observed underwater holding stations above the substrate and feeding in midday, when water temperature was <4°C (Cunjak, unpublished data) in the autumn. These observations were coincident with the spawning period of adult Atlantic salmon in the stream and may have been a periodic response to the sudden availability of a high quality food (eggs) for consumption.

Fig. 1. Conceptual representation of biophysical phases of winter depicting generalized pattern of discharge and water temperature in relation to freshwater lifestages (egg, parr, and kelt) of Atlantic salmon in ice-covered rivers. PBU = pre-break up and BU = break up. Sizes and placement of boxes correspond to timing and duration of the described events. Abbreviations: scour = ice scour; disturb = disturbance; dewater = dewatering; turbid = elevated turbidity.



During the early winter, metabolic rates of fish decline because of changes in photoperiod (Evans 1984), as well as, temperature. Higgins and Talbot (1985), in studying Atlantic salmon growth in freshwater, found a greater linkage between growth and photoperiod than growth and water temperature. The presumed mechanism was that photoperiod altered the endogenous rhythm of appetite and growth (Villarreal et al. 1988). Seasonal changes in gut evacuation rates of salmon that occur as a result of a lower metabolic rate were suggested to be neural or hormonal and, therefore, are affected by photoperiod (Higgins and Talbot 1985). Photoperiod is a more reliable cue for impending seasonal changes and, thus, physiological acclimation rather than responding only to declining temperatures that are extremely variable (Wootton 1990).

Although salmonids remain "active" during winter (i.e., do not exhibit torpor, Crawshaw 1984), it is the reduced assimilation efficiency and slow gut evacuation rates at low winter temperatures, and not food resources, that appear to be the limiting factors to meeting the physiological demands of cold acclimation in early winter (Fry 1971; Cunjak et al. 1987; Cunjak 1988*b*). The reduced appetite or "anorexia"

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reported by Metcalfe and Thorpe (1992) for young-of-the-year (YOY) salmon in early winter was regulated by the nutritional state of the fish. Further, these authors found that this anorexia was most pronounced among smaller members of the age-class and suggested this to be a tactic to minimize energy expenditure as these fish would not smoltify the following spring. During this stressful transition time (cold acclimation, Fig. 1), salmonids lose the greatest amount of lipids (brook trout and brown trout, *Salmo trutta*: Cunjak 1988*b*; Atlantic salmon: Gardiner and Geddes 1980; Sutton 1994). A recent model (Bull et al. 1996) corroborated these findings and showed that appetite was regulated adaptively in accordance with long-term energy requirements rather than short-term needs.

Of particular relevance to the topic of winter nutrition is the energetic value of egg consumption by parr, and specifically for the winter survival of pre-smolts. Largely speculative at this point, the story is nevertheless intriguing. Eggs have a high lipid content and are easily digestible. Their availability in early winter when physiological demands (i.e., for cold acclimation, Cunjak 1988*b*) are high, would make egg consumption an adaptive trait particularly if winter survival is strongly related to the acquisition of a threshold energy level (Gardiner and Geddes 1980). The problem of insufficient reserves for overwintering is most critical for post-spawned male parr and is the basis for the theory of high winter mortality at this life-stage (Dalley et al. 1983; Myers 1984; Prévost et al. 1992). Yet, some spent parr do survive winter and can even complete smoltification, as evidenced by milt production among early smolt migrants in Canadian and New England streams (R. Saunders, Canada, personal communication; Whalen 1998) and in Europe (Jones 1959; Berglund 1992). It may be that winter survival by some pre-smolts (especially spent male parr) or "upper mode" parr (*sensu* Thorpe 1977) is partly dependent on the acquisition of energy reserves provided via egg consumption in early winter. The relevance of this topic to smolt physiology, winter survival and life history theory, is deserving of future research.

Nutritional insufficiencies and parasite loads can act as stressors that debilitate young salmon and may result in winter mortality. Pickering and Pottinger (1988) found winter mortality among YOY salmon to be greatest for the smallest fish and attributed this to chronic stress resulting from a nutritional deficiency as measured by body condition, blood cell counts and cortisol levels. A study (Cunjak and McGladdery 1991) on the effect of glochidial parasitism on the gills of overwintering juvenile Atlantic salmon in a Nova Scotian river showed that heavy parasite loads were contributing to the poorer body condition and smaller size in salmon parr. This glochidia–salmon relationship is not unique to North America but shows a holarctic distribution extending through the U.K., and Russia (Ziuganov et al. 1990). Recent observations (Table 1) of a marked increase in the number of leeches (Hirudinea) attached to the body and fins of wild Atlantic salmon parr in early winter may further stress these fishes at this critical period of the year. It is interesting that the incidence of leeches is most prevalent in Atlantic salmon (Cunjak, unpublished data) and coincident with the time of year that the fish move beneath rock shelters, perhaps where they are more susceptible to attachment by the ectoparasites. The effect of leeches on winter survival is presently unknown but a related species of hirudinean has been identified as the vector of a hemoflagellate parasite in Pacific salmon (Bell and Margolis 1976).

Table 1. Frequency and incidence of leeches (*Piscicola punctata*) on the fins and body of Atlantic salmon parr collected from Catamaran Brook, 1993–1995.

Season	*N*	Parr with leeches (%)	Mean incidence per parr
Summer	3532	0	0
Early winter	2548	186 (7.3)	1.2
Spring	451	0	0

Note: *N* = number of parr examined.

Ice initiation and freeze-up

Once the water temperature reaches 0°C in a river, the first ice usually forms along the banks. Once the bank material is cooled below its threshold temperature, ice crystals will begin to nucleate and grow laterally across the surface into the main channel. Conditions are most suitable for this lateral growth where the flow is essentially laminar in the less turbulent reaches. Localised "border" ice growth may also occur well away from the shore around obstacles such as exposed boulders that create their own unique set of flow and thermal conditions.

During the early stages of freeze-up, all forms of border ice may provide overhead cover for stream salmonids in otherwise open stretches of stream (e.g., Maciolek and Needham 1952; Brown et al. 1994; Cunjak 1996). Parr may use ice cover when not occupying substrate shelters (Whalen 1998) whereas post-spawning salmon (kelts) have been observed resting beneath shelf ice (Cunjak, personal observations), which could serve the dual purpose of predator avoidance and energy conservation.

Although the entire channel width of some streams and small rivers may be covered by the gradual outward progression of border ice, especially under very cold meteorological conditions, increasing flow turbulence halts its lateral growth. In these turbulent areas, ice formation typically occurs by nucleation of small "frazil" particles (see Tsang 1982, typically 0.1 to 5 mm diameter) at a small degree of supercooling (~–0.1°C, see Fig. 1). Rapid secondary multiplication of additional frazil crystals can quickly result in high concentrations (e.g., as high as 10^6 m^{-3}; Gilfilian et al. 1972). While the crystals are in a supercooled or "active" state, they continue to grow and may adhere to one another or bond to other objects.

Under very cold winter conditions, frazil may be generated during the daytime but in general the formation follows a diurnal cycle characterized by rapid growth at night and a cessation during the day, due primarily to warming by solar radiation. Highly turbulent open-water reaches, such as found at riffles and rapids, create the best set of flow conditions for the generation of large amounts of frazil. Much of the frazil generated at such sites is subsequently deposited beneath ice cover in pools downstream. Where rapids remain open for protracted periods, large frazil accumulations

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known as "hanging dams" can virtually fill pools (Michel and Drouin 1981; Beltaos and Dean 1981) and lead to the main flow being channelled down to the pool bottom where frazil ice and high velocities can scour the substrate.

Recent radio-tagging studies of stream salmonids have related their movement to frazil ice. Brown and Mackay (1995) found cutthroat trout, *Oncorhynchus clarki*, avoided frazil deposition in pools in an Alberta river. Jakober et al. (1998) noted greatest winter movement by bull trout, *Salvelinus confluentus*, and cutthroat trout in those Montana streams where subsurface ice formation and supercooling were most common. Atlantic salmon kelts in the Miramichi River (Komadina-Douthwright et al. 1997), monitored over two winters, emigrated from tributary streams (<4th order) to main river channels immediately after spawning. These kelts quickly moved downstream (Fig. 1) to overwinter in backwater habitats, in the lee of islands or below the head of tide. In these areas, Komadina-Douthwright et al. (1997) speculated that ice, mainly frazil accumulation, would be reduced, and current velocities were low enough to ensure that energy expenditure was minimized. Main river pools, by contrast, were often choked with frazil ice reducing habitat suitability (Cunjak and Caissie 1994; Komadina-Douthwright et al. 1997).

In the more shallow turbulent reaches of a stream or river, active frazil ice and its associated supercooled water can be conveyed to the channel bottom where it can lead to the formation of "anchor" ice. Although such ice may adhere to almost any object, it most commonly bonds to aquatic vegetation, boulders, and even large areas of gravel and coarse sand. Given the right set of flow and weather conditions, anchor ice can spread and thicken over quite large portions of the channel bed. Calkins and Brockett (1988) and Whalen (1998) noted that 95–100% of the stream-bed of Atlantic salmon streams in New Hampshire and Vermont were blanketed with anchor ice prior to the formation of a continuous surface ice sheet. As long as conditions remain cold, anchor ice will only release when buoyancy is sufficient to lift the underlying bed material. Although such releases have frequently been cited as affecting the available invertebrate drift (e.g., Maciolek and Needham 1952; Miller and Stout 1989) the main ecological impact of anchor ice results from its effect on organisms within the bed material, particularly eggs and alevins. This can be either from a direct impact, such as through in situ freezing (Walsh and Calkins 1986) or indirectly through a restriction or elimination of flow (Fig. 1) and associated dissolved oxygen through the substrate (e.g., Calkins 1989; Power et al. 1993).

Earlier, we indicated that the location of salmon redds in midstream was adaptive in relation to flow hydraulics. The location of redds is not, however, without potential disadvantages given the unique physical conditions characteristic of early winter. Reiser and Wesche (1979) found eggs of brown trout buried 15 cm in the substrate to freeze despite 12–20 cm of water flowing over the redd in a Wyoming stream. This can likely be explained as intrusion of supercooled water into the interstitial spaces of the redd which subsequently froze as velocity was reduced. This form of subsurface ice would presumably be more deleterious to eggs (than frazil penetration) because of the denser nature of the ice. Such supercooled water penetration was noted in an Atlantic salmon stream in Vermont (Calkins 1989) but any effect on stream biota has yet to be confirmed.

Frazil ice crystals travelling with the flow continue to grow and agglomerate into larger flocs and become increasingly buoyant and less controlled by river turbulence (Tsang 1982). Eventually these crystals grow to sufficient size and concentration to arch across the river width, usually at some channel constriction often associated with encroaching border ice. Unless entrained by high flow velocities beneath this initial ice cover, subsequent incoming ice floes will begin to pack in and accumulate upstream forming a freeze-up ice cover. Formation of this initial, often very rough, ice cover can produce major changes to the flow regime as a result of the hydraulic storage of water (e.g., Gerard 1990; Prowse 1994; Gray and Prowse 1993). Consequently, upstream increases in water levels are often quite dramatic and have been cited as important in supplying water to aquatic habitats located along channel margins and in the floodplain (e.g., Paschke and Coleman 1986; Burn 1993). Concomitant with the increases in upstream water levels are the associated reductions in downstream discharge (Fig. 1). Although relatively short-lived, such ice-induced low-flow events can be lower than the more commonly recognized low-flow periods that occur in late winter as a result of minimal catchment runoff (Fig. 1). Periods of low flow have a number of important biological implications and many of these occur during the ice season when biological activity (and response) is slowed, or arrested, by low temperatures.

Midwinter

This period is typically characterized by declining water levels and stable near-freezing water temperatures (Fig. 1). In temperate-maritime regions, salmon rivers may develop only a partial ice cover or be intermittently ice covered during especially cold periods. In colder regions, however, a complete ice cover can develop and persist for several months. It is in these latter systems that ice becomes a dominant factor affecting the type and availability of stream habitat, including related factors such as light and oxygen levels and flow patterns.

Ice growth and habitat reduction

Once an ice cover has developed, water temperature remains close to 0°C (i.e., typically less than a few hundredths of a degree above freezing, Fig. 1). Any heat input by, for example, groundwater or radiative warming, is rapidly transferred by turbulent mixing to the overlying ice: the rougher the ice subsurface, the more rapid the heat transfer. Even though water temperatures may only be a fraction of a degree above freezing, the flow velocity can promote a rapid transfer of heat. Marsh and Prowse (1987), for example, found the water-to-ice heat transfer beneath a solid river ice cover to vary from approximately 10–30 $W \cdot m^{-2}$ with water temperatures of only 0.003–0.01°C. During midwinter, the magnitude of this water-to-ice hydrothermal flux is dwarfed by the large ice-to-atmospheric heat loss that promotes ice growth.

The growth of ice proceeds vertically downward into the water column. Growth rates can be accelerated by the presence of frazil deposited beneath the ice cover and retarded by the insulating effects of snow. With continued ice growth,

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an increasing portion of shallow water areas becomes frozen to the bed and the flow becomes increasingly concentrated in the deeper portions of the channel. Habitat reduction is further exaggerated by the deposition of frazil ice that tends to accumulate in low-velocity, marginal areas of the flow. The loss of river margin habitat may partly explain the redistribution and midstream concentration of salmon parr found sheltering beneath rocks during daytime in winter (Cunjak 1988*a*). In a section of a Vermont river, Whalen (1998) found that ice reduced the abundance of parr habitat such that the most commonly selected microhabitats represented <10% of those recorded when ice was absent.

Extensive frazil accumulations beneath ice cover can result in available habitat being largely restricted to the main flow channel and associated deep pools. Research by Calkins (1989) in New England salmon rivers found that ice could occupy 60–80% of the cross-sectional area of small to medium-order streams. Cunjak and Caissie (1994) found that 73–83% of the volume of a large (13 375 m^2) pool in the Miramichi River was occupied by frazil ice throughout the winter. Subsequent surveys in other main river pools in the Miramichi River found similar frazil accumulations (Komadina-Douthwright et al. 1997).

Such ice accumulation and associated habitat restictions may partly explain the winter movement patterns of fishes noted in recent years. Scruton et al. (1997) found landlocked Atlantic salmon kelts in a regulated Newfoundland river system moved considerable distances soon after spawning, and just prior to freeze-up, to subsequently overwinter in lakes. In the Miramichi River, radio-tagged Atlantic salmon kelts moved less in midwinter than early winter just prior to freeze-up (Table 2). Once a solid ice cover formed on the river, movements rarely exceeded 0.5 km per week (Komadina-Douthwright et al. 1997). An interesting finding was that most of the kelts (both years) moved to overwinter below the head of tide where presumably ice conditions and frazil accumulation would be reduced by tidal action. Longest winter movement was by those kelts which were farthest above head of tide (Table 2). Once in tidal water, kelts rarely returned upriver.

Under extreme ice conditions and reduced habitat availability, young salmon would be required to move to more suitable overwintering areas. In so doing, they might expend critical energy reserves. In northern rivers such as the Varzuga River (Kola Peninsula, Russia), it is possible that extensive freezing of the smaller tributary streams may limit accessibility in winter by stream fishes. This may partly explain the relatively greater biomass and productivity found in the main Varzuga River compared with the tributaries (Kazakov et al. 1992). By contrast, in the River Teno in Finland, tributary streams provide the most suitable winter habitat (coarse substrate and warmer water) for parr and may explain the movement of parr ≥1+ into these streams from the main river (Erkinaro 1995). In several ice-covered, eastern Canadian rivers, Cunjak and Randall (1993) found that winter movement by juvenile Atlantic salmon was significant, and site fidelity appeared to be related to the availability of suitable winter habitat. In relatively stable, cobble-bottomed stream sites, 19–30% of the original (early winter) population was recaptured compared with only 2% in a stream site where suitable winter habitat was scarce and where anchor ice formation was extensive.

As discharge declines during the ice growth period, the ice cover periodically fails along bank support zones (Billfalk 1981) and falls to the level of the new, lowered water surface. This does not tend to occur on streams where the narrowness of the channel or the positioning of numerous large boulders permits the cover to remain intact and suspended at or near the original freeze-up level. The air cavities beneath these suspended covers have a unique microclimate, insulated from the extremes of cold winter air temperatures yet warmed by the penetration of solar radiation. The biological significance of these air-gaps is yet to be studied although fish-eating mammals such as mink (Calkins et al. 1989) and emerging stoneflies (Pugsley and Hynes 1986) use such habitats in winter.

In addition to reduction in habitat *availability* (Fig. 1), another form of habitat change in winter is reduction in *suitability*. Once an ice cover blankets the water surface, gaseous exchange with the atmosphere is eliminated and photosynthesis is slowed. As winter progresses, dissolved oxygen levels typically fall because of an increase in the proportion of groundwater to streamflow and because of oxygen consumption by various biochemical processes (respiration and decomposition) within the water column and sediment. The latter is enhanced by an increase in the residence time (relative to open-water conditions) because of the decline in velocity induced by a surface ice cover. Anoxic (or very low dissolved oxygen) conditions in rivers beneath ice cover have been documented from geographically distant regions (e.g., Hynes 1970; Ranjie and Huimin 1987; Ultsch 1989) but appear to be most prevalent in higher latitudes (Schreier et al. 1980; Bendock 1981) where ice cover persists for longer periods. Winter depressions in dissolved oxygen can be exaggerated by anoxic groundwater intrusions and can reach concentrations which are lethal to young salmonids and eggs (Bustard 1986; Adams and Cannon 1987; Lacroix 1985). Schmidt et al. (1989) reported on an extreme situation of depleted oxygen (1.1 $mg \cdot L^{-1}$) in the Sagavanirktok River delta, Alaska, which resulted in mortality for fish (mainly round whitefish, *Prosopium cylindraceum*) that were crowded in the pool because of restrictive ice conditions and low streamflow. To date, there have been no published accounts of winter anoxia beneath an ice-cover in Atlantic salmon rivers. In Catamaran Brook, sub-ice oxygen concentrations were measured frequently over one winter in inundated main-channel beaver ponds but dissolved oxygen remained above 79% saturation (Komadina-Douthwright 1994).

Winter duration, fish condition, and body size

Lipid levels at the onset of winter have been linked to survival of many young-of-year fishes (e.g., brook trout: Toneys and Coble 1980; largemouth bass, *Micropterus salmoides*: Sullivan 1986; Ludsin and DeVries 1997; smallmouth bass, *Micropterus dolomieui*: Oliver et al. 1979; yellow perch, *Perca flavescens*: Toneys and Coble 1980; Sullivan 1986). In a comparison of lipid storage and use, Sullivan (1986) found that largemouth bass stored lipids in viscera and muscle whereas yellow perch stored fat mostly

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Table 2. Timing of winter movement and average distance (km) travelled by wild, radio-tagged Atlantic salmon kelts in three pools in the Northwest Miramichi River where fish were originally tagged and released following spawning (1993–1994 and 1994–1995).

	Miner's Pool	Big Hole (1993–1994)	Big Hole (1994–1995)	Craig Pool
Early winter	–26.8	–6.1	–7.8	–4.6
Mid-winter	–5.5	–3.6	+0.5	–0.8

Note: Negative numbers represent net downstream movement; positive values, net upstream movement. Pools are arranged according to distance from head-of-tide with Miner's Bridge Pool being most upriver site.

in viscera and gonads, which explained why yellow perch must feed all winter and were more prone to starvation. Bass, because they do not feed, are more sensitive to long winters (Sullivan 1986). Atlantic salmon parr may adopt an intermediate mode of using lipids. That is, they continue to feed to some degree (Riddell and Leggett 1981; Cunjak 1988*a*) like yellow perch, but salmon also reduce their activity, similar to the mode of energy conservation noted for bass. Such an intermediate mode of limited feeding and activity adopted by salmon may be the most prudent approach to survival in the demanding winter environment of running waters (Fig. 1).

Another aspect of winter survival is the notion of size-selective mortality in fishes in relation to lipid use and energy efficiency. This factor is most pertinent to fish in their first year of life. In age-0 largemouth bass, lipids regulated size-related winter mortality directly because earlier-hatched bass grew faster, switched to eating fish earlier, and stored more lipids in the fall (Ludsin and DeVries 1997). Survival was greater for larger yellow perch than smaller ones and was thought to be related to loss of fat stores because survivors had higher fat contents than those that died (Toneys and Coble 1980). Hunt (1969) determined that there was a positive relation between size and winter survival in brook trout to which he suggested the probable mechanism was energetic efficiency at low temperatures. In Atlantic salmon, larger fish have greater fat stores (Metcalfe and Thorpe 1992). In a hatchery study, Lindroth (1965) found that the largest YOY salmon suffered the least mortality over winter, which he related to size position within a year class and not absolute size *per se*, a contention supported by the work of Reimers (1963) and by the threshold concept expressed by Toneys and Coble (1980).

Cunjak and Randall (1993) speculated that large body size may affect winter survival as a result of a competitive advantage over smaller conspecifics that are subsequently displaced from limited winter habitats. They found that by late winter, the mean size of resident YOY salmon was consistently larger than that of immigrant YOY within similar habitat types of three Canadian streams. Experiments with some salmonid species have shown that those individuals introduced to a new location experience higher mortality rates than resident fish (Noakes 1978), perhaps because of risk associated with moving to unfamiliar areas (Dolloff 1987). The concept of competition for limited winter habitat suggests a potential for aggressive interaction as was recently quantified by Gregory and Griffith (1996) for YOY rainbow trout (*Oncorhynchus mykiss*). They found that larger individuals successfully displaced smaller YOY and were more aggressive near dawn when fish were seeking daytime concealment cover. Atlantic salmon parr, which also seek daytime concealment cover in winter, may experience similar competition.

Atlantic salmon have complex life histories (see Hutchings 1998, this issue) in which size-selective winter mortality and lipid levels are likely also affected by parr maturation. Between summer and autumn, individually marked mature parr in Vermont grew approximately half as fast as immature parr (Whalen 1998). By February, lipid levels were lower for mature parr than immature parr (S. McCormick, personal communication). Males (which were mostly mature) had lower lipids than females in November, and in April (Sutton 1994). The acknowledged high rate of mortality among mature male Atlantic salmon parr in winter (Mitans 1973) has been attributed to insufficient energy reserves having been accumulated after spawning and particularly if attempting to smolt the following spring (Dalley et al. 1983). This phenomenon led Myers et al. (1986) to suggest a size threshold of 70–72 mm below which male Atlantic salmon cannot mature and subsequently overwinter. Winter duration was also found to be a contributing factor to the incidence of maturity among 1+ Atlantic salmon males from a Newfoundland river (Prévost et al. 1992) probably because of the consequent reduction in growing opportunities necessary to achieve maturation (see Berglund 1992).

For Atlantic salmon kelts, post-spawning survival is generally highest in northern latitude streams of North America and Europe (Fleming 1996) where winters are cold. Mortality of male and female kelts in a river in France was found to occur within 2 weeks following spawning (Baglinière et al. 1990, 1991). This rapid mortality may be related to a combination of relatively warm water temperatures (7–10°C) necessitating a higher metabolic rate (and demand) and a weakened condition exacerbated by spawning lesions and subsequent infection by *Saprolegnia* fungi such as are common in southern European salmon rivers (J.-L. Baglinière, France, personal communication). In the River Dee in Scotland, previous-spawners represented only 9.7% of returning large salmon for 1992–1994 (Anonymous 1996) suggesting a low level of kelt survival relative to Canada (Table 3). Similar low percentages of previous spawners for rivers in the U.K. were noted by Jones (1959).

Some of the between-river variation in the percentages of repeat-spawners (Table 3) may be attributable to the nature of the riverine environment where post-spawned salmon must overwinter. Among the Newfoundland rivers, Pinware River had the lowest representation of previous spawners in samples of large salmon (>63 cm); it is the most northerly

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Table 3. Percentage representation by repeat-spawners in the spawning population of multi-sea-year (large) Atlantic salmon in rivers of Newfoundland (NF), Labrador (LB)) and New Brunswick (NB).

River	Province	Years of data	*N*	% repeat spawners
Western Arm Brook	NF	15	90	78.9
Torrent	NF	12	185	61.6
Harry's	NF	4	18	55.6
Humber	NF	14	496	51.4
Lomond	NF	10	53	22.6
Pinware	LB	13	329	9.7
Big Salmon	NB	3	230	85.2
Nepisiguit	NB	6	2110	53.7
Miramichi	NB	10	n/a	34.5
Restigouche	NB	6	1470	30.3
Buctouche	NB	2	114	21.8

Note: Sources: Mullins 1997; Mullins et al. 1997; C. Mullins, personal communication; Chaput et al. 1994; Ducharme 1969; Atkinson and Chaput 1995; Atkinson et al. 1997; Mowbray and Locke 1996; A. Locke, personal communication). *N* = total number of large salmon sampled for the period. n/a = no data available.

river in the list (in Labrador) and is a generally shallow river of high gradient. Western Arm Brook, a northern river of insular Newfoundland, is characterized by many lakes where kelts often overwinter (Lévesque et al. 1985; Scruton et al. 1997) and has a high percentage of repeat spawners which suggests good winter survival. Among the New Brunswick rivers, repeat-spawners are relatively scarce in the Buctouche River where the river is short, shallow, has little pool habitat, and which remains ice-covered for >4 months. The Humber, Nepisiguit, Miramichi, and Restigouche rivers are large rivers with complex river channels offering a variety of suitable overwintering habitats despite prolonged ice conditions. The Big Salmon River in southern New Brunswick is within the drainage of the Bay of Fundy, which significantly moderates the winter climate (i.e., minimal ice accumulation) and may partly explain the high survival of kelts in this system.

Break-up/warming

Most winters in temperate latitudes, are characterized by periodic melt periods. The more temperate the climate, the greater the probability that such warming will be of sufficient duration to initiate a break-up of the ice cover. In colder climates, midwinter break-ups are rare. Instead, ice break-up is usually confined to late winter (Fig. 1). Regardless of the seasonal timing, break-up of an ice cover is often the most significant hydrologic event of the year. From a "disturbance" perspective (*sensu* Sousa 1984, Resh et al. 1988), break-up has a much greater potential than open-water floods to reset the biotic template in both the channel and in adjacent floodplains (Gatto 1993; Scrimgeour et al. 1994; Prowse 1994; Prowse et al. 1996). This section reviews our current biophysical understanding of the significance of the melt and break-up phases, and is followed by a first-ever case study of the importance of interannual variations in break-up intensity on survival estimates of juvenile Atlantic salmon.

Snowmelt and pre-break-up

The late winter period on ice-covered systems begins with a sustained melt of the winter accumulation of snow and a related increase in river discharge (Fig. 1), velocity and water levels. Stream water quality may rapidly change during this period depending on the chemical composition of the ablating snowpack. In essence, a stream can receive the entire winter chemical load of wet and dry atmospheric deposition within a few days.

Snowmelt events have been shown to severely impact Atlantic salmon egg and alevin survival because of the undiluted nature of the low pH water entering streams (Haines 1981; Rosseland and Skogheim 1984; Lacroix 1985; Gunn 1986). In the case of southwestern Nova Scotia salmon streams where local geology offers little acid-neutralizing capacity, greatest pH depressions occurred in midwinter as a result of acidic rain that is more acidic than the snow (Watt et al. 1983). Recently hatched sac-fry (alevins) tend to be most sensitive to low pH (Daye and Garside 1979; Korman et al. 1994) and their arrival is, unfortunately, often coincident with snowmelt-mediated pH depressions (Gunn 1986). In Atlantic salmon rivers in Norway, it was the pre-smolt stage that was most sensitive to low pH snowmelt water (Rosseland and Skogheim 1984). In general, the situation for affected salmon rivers such as in southwestern Nova Scotia may be improving as atmospheric sulphate levels decline (Watt 1997).

Whereas midwinter was dominated by groundwater inputs (baseflow), the increase in surface melt reverses this situation and can even lead to a hydraulic displacement of groundwater through a reversal in flow directions. It has been shown, for example, that rising stage can lead to surface water penetrating deeper into substrate areas normally fed by groundwater inflow. Because there is generally a temperature difference between the two flows, such a flow reversal can have a direct thermal impact (cold shock) on biota inhabiting the substrate. Laboratory experiments with developing Atlantic salmon eggs noted slower growth and increased mortality for eggs and alevins exposed to sudden decreases in temperature (Peterson et al. 1977).

Although stream water temperatures remain very close to freezing during the melt period (Fig. 1), even minor changes (<0.1°C) in the temperature of rapidly flowing water can produce rapid thinning of the base of an ice cover. This, accompanied by changes in ice strength due to radiative heat-

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ing (Ashton 1985; Prowse et al. 1990), hastens the onset of river ice break-up.

Break-up and disturbance

Break-up is commonly classified into two types based on associated hydrometeorological conditions: premature or dynamic, and over-mature or thermal. In the case of thermal break-up (which is common to lakes), streamflow increases tend to be small because of a shallow snowpack or protracted melt. This in turn permits the ice sheet to become extensively melted and structurally weakened before the ice is finally dislodged. Although some minor ice jamming may occur, increases in water level and physical disruption of the channel are minimal.

Quite a different set of conditions governs dynamic break-up. Such events are characterized by large and rapid spring runoff, especially when the melt process is assisted by substantial rainfall. So abrupt is such melt that the ice cover has little time to decay and, hence, offers maximum resistance to the downstream passage of the flood wave. Its subsequent downstream progression into more intact ice is typically characterized by a series of stalls and surges associated with the repetitive formation and release of thick ice jams (Beltaos 1995). Water stored behind these stalling ice jams often produces extensive flooding of the channel and adjacent floodplain. Notably, water levels produced by break-up events far exceed those possible under open-water conditions for equivalent discharge. Common ice-jamming sites include those where the channel planform obstructs ice movement, such as at river bends, meanders, and islands, and where the slope quickly decreases and the channel widens (e.g., at stream mouths entering larger ice-covered rivers and lakes). Ice-jam flooding, which rapidly increases the amount of available corridor and riparian habitat, is usually short-lived and is even more quickly reduced with the sudden drawdown of water associated with the subsequent release and downstream surge of the ice jam.

The surge of ice and water produced by the sudden rupture of an ice jam can have a significant impact on the downstream channel and banks. Again, the magnitude and velocity of such events can far exceed those occurring under natural open-water conditions. For example, break-up surge velocities in excess of 5 $m \cdot s^{-1}$ are not uncommon for dynamic break-ups (e.g., Doyle 1977; Gerard 1975; Prowse 1984; Ferrick et al. 1992). Such surges can be an important agent of erosional and depositional change, especially on alluvial rivers. In terms of bed-load transport, shear stresses associated with rapidly moving breakup fronts have been estimated to be able to move material as large as 0.2 m in diameter (Beltaos 1993). Under such high conditions of bed transport, it is likely that main channel habitats and associated biota would be severely disrupted. Just prior to, and during, ice break-up in the Northwest Miramichi River in 1995, radio-tagged salmon kelts were generally found near tributary mouths, point sources of groundwater (spring) discharge, and in backwater channels (Komadina-Douthwright et al. 1997). These sites (tributaries and back-channels) may provide refugia during the period of most dynamic break-up and related scour. Clifford (1969) suggested a similar tactic for leptophlebid mayfly nymphs, which he observed migrating into tributaries of an ice-covered Alberta stream in April, just before break-up.

Break-up fronts (moving transition zone between intact and fractured or fragmented ice) typically result from surges (river waves) produced by the dramatic failure of upstream ice jams (e.g., Beltaos and Krishnappen 1982; Henderson and Gerard 1981). In Atlantic salmon rivers in New England, Calkins et al. (1989) observed ice-push at break-up fronts of sufficient force to move 70 kg boulders and, therefore, capable of dislodging shelters (Fig. 1) and injuring fishes such as dace, cottids, and salmonids (eggs and parr), which typically overwinter within the substrate (Cunjak 1996). Commonly associated phenomena such as flooding and ice-jams can result in displacement and mass stranding of riverine species, which eventually suffocate as water levels recede.

Ice abrasion and high-velocity scour of the bank and channel substrate can also lead to very high suspended-sediment concentrations, as much as several times that for equivalent discharge under open-water conditions (Prowse 1993; Beltaos et al. 1994; Milburn and Prowse 1996). Subsequent resettling of this material can coat the bed and banks in a veneer of sediment. Accumulations of as much as 1 m deep have been observed at the edge of levees (Eardley 1938) but no published data are available about the thickness of in-channel coatings. The tenure of such sediment probably depends on the timing of breakup relative to subsequent spring increases in discharge.

Temperature increase and warm acclimation

Although temperatures beneath lake covers are known to climb to several degrees above freezing (Marsh and Prowse 1987), under-ice water temperatures in a river rarely climb above a few hundredths of a degree, except in cases of significant inflow of warm water from tributaries or groundwater, or in streams where an air gap may exist between the ice and water surface. Near-freezing temperatures are usually maintained because of the rapid heat transfer to the ice promoted by turbulent flow conditions (Fig. 1). At the time of break-up, however, very rapid changes can occur in water temperature. Changes are most pronounced in the case of dynamic break-ups because of the extensive open-water reach upstream of the main break-up front. Within this usually turbid zone, water is rapidly warmed by heat exchanges with the atmosphere (Prowse 1990). Measurements on large rivers have reported temperature increases of as much as 3 to 9°C (Parkinson 1982; Prowse and Marsh 1989) at the interface between open-water and the upstream edge of ice break-up. Smaller changes are expected on smaller rivers and streams where the biological implications are probably just as significant but, as yet, poorly understood. For example, substrate decomposition rates increase with water temperature in late winter and early spring with concomitant declines in dissolved oxygen and CO_2 (Peterson et al. 1982). Both variables can affect Atlantic salmon alevin survival, particularly where gravel permeability is reduced by fine sediment deposition (Peterson 1978), and where pH is low (Gunn 1986).

Following the abrupt change in water temperature associated with the passage of the break-up front, direct atmospheric heating of the open water resumes. In general,

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increases in spring water temperatures tend to parallel those of air temperature but can exhibit increases when high turbidity associated with the break-up front enhances absorption of radiant energy in the water column (see Scrimgeour et al. 1994). The period of "warm-acclimation" is not as physiologically demanding as cold-acclimation (early winter) except that fish are starting from an already depleted condition having survived to late winter (Fig. 1). During the warming phase associated with break-up, parr that managed to survive the winter are faced with replenishing depleted lipids. The appetites of Atlantic salmon parr are geared to follow seasonal trajectories where lipids are lowest at the beginning of spring (Bull et al. 1996). Improved environmental conditions and feeding opportunities following late winter typically allow for a rapid increase in body lipids (Cunjak 1988*b*; Cunjak and Power 1987). In Newfoundland, lipids from Atlantic salmon rebounded from a winter low of ~ 6% in April to over 13% by June (Sutton 1994); in Vermont, the largest increase in lipids, on an annual basis, occurred in Atlantic salmon pre-smolts between February and April (S. McCormick, personal communication).

Warm-acclimation may be most difficult for kelts that are in poor condition by spring after fasting all winter, and mortality may occur at this time (Lévesque et al. 1985) as they try to resume feeding (Fig. 1). In a laboratory experiment to recondition Atlantic salmon kelts, Crim et al. (1992) found that kelts that failed to feed eventually lost weight and died, but only as water temperatures began rising. In general, however, winter survival in freshwater seems to be relatively high in most Canadian rivers based on the high percentage of repeat spawners among large Atlantic salmon in many populations (see Table 3 and earlier section). A mark-recapture experiment of post-spawned salmon in Western Arm Brook, Newfoundland, provides further evidence. At a counting fence in early spring for two consecutive winters, 37 and 47%, respectively, of kelts (marked as spawning adults the previous autumn) were recaptured (C. Mullins, Canada, personal communication). These survival estimates were minimum values as trap operation was dependent on water/ice conditions and likely missed the earliest emigrants (May). In fact, Chadwick et al. (1978) estimated winter survival of kelts in Western Arm Brook as high as 88% probably because of the abundant lacustrine habitat in this system where kelts prefer to overwinter (Lévesque et al. 1985; Scruton et al. 1997).

The availability of forage fishes following ice break-up has been suggested to be critical to the ultimate survival of kelts as they prepare to return to sea (Moore et al. 1995). In support, radio-tagged kelts in the Northwest Miramichi River showed a net upstream movement only 3 days after ice break-up (Table 4) and coincident with the start of the upstream migration of rainbow smelt, *Osmerus mordax* (Komadina-Douthwright et al. 1997), a favoured prey of salmon kelts. This was the first net upstream movement in several weeks by kelts.

Catamaran Brook case study — impact of variable winter conditions

The data collection and ongoing multidisciplinary research in the Catamaran Brook basin of New Brunswick (Cunjak 1995) lends itself to a detailed analysis of interannual variability in YOY Atlantic salmon abundance, and for deriving hydro-ecological explanations for the variability. Using counts of female spawners entering the brook and passing through the counting-fence each autumn (Hardie et al. 1998) and estimates of size-derived fecundity, egg deposition was calculated for each spawning cohort from 1990 to 1995 (Cunjak and Therrien 1996, 1998). These values were then related to annual estimates of YOY abundance in the brook (by electrofishing) approximately 1 month post-emergence (Cunjak, unpublished data). Electrofishing was conducted each summer, using barrier nets, by an experienced crew of 3–4 people in 26–32 sites. Estimates of population abundance were derived using a multiple sweep removal method. Corrections for "loss" of recently emerged fry from the brook via drift emigration in the first month of life were applied (Johnston 1997) in order to provide an estimate of the fry abundance in the brook immediately following emergence from redds (mid-June). Fry abundance was then compared with egg deposition (from previous November) to provide a measure of first winter survival.

Table 4. Distance moved (km) by 12 radio-tagged Atlantic salmon kelts in the Northwest Miramichi River between April 20 and April 25, 1995, the period of ice break-up in the river. Negative numbers represent net downstream movement; positive values are net upstream movement.

	Before (1 day)	Ice-out	After (3 days)
Average movement	–0.5	–0.7	+0.2
Maximum movement	–3.9	–1.6	+1.8

The number of salmon fry surviving winter to emergence in Catamaran Brook between 1991 and 1996 was poorly explained by egg deposition the previous autumn ($r^2 = 0.001$). Fry numbers resulting from the 1994 and 1995 spawning cohorts were similarly very low although they originated from markedly different egg depositions (Table 5). The low number of emergent fry from the 1994 cohort was readily explained by the low number of adult females ($n = 27$, compared with 84 females in 1995) that spawned in a restricted area as a consequence of unusually low water conditions that autumn (Fig. 2) and a beaver dam barrier to migration at river km 0.8 (Cunjak 1995). The poor winter survival of fry from the 1995 spawning cohort could not be so readily explained, as egg deposition was extremely high and water conditions (late October – early November) were sufficient that spawners were able to access >8 km of stream. The poor survival in 1995–1996 was especially problematic relative to the 1992 cohort that deposited a similar number of eggs (Table 5) under similarly moderate flow conditions in early winter (Fig. 2) but the 1992 cohort produced many more fry that survived to emergence (Table 5).

Density-dependent survival was unable to account for most of the variability in the data when egg density was regressed with survival to emergence ($r^2 = 0.31$). For most years, egg deposition was at moderate densities (3.1–7.0 eggs·m^{-2}, Table 5). These densities were within the range of suitable "target" egg depositions noted for Atlantic salmon (see reviews by Symons 1979; Kennedy and Crozier

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Table 5. Annual estimates of egg deposition, egg density (no.·m^{-2}), emergent fry, and winter survival (egg to emergence) for Atlantic salmon in Catamaran Brook, 1990–1995.

Spawning year	Egg deposition	Egg density[a]	Emergent fry	% survival to emergence
1990	269 526	3.2	164 436	61
1991	375 562	4.5	93 665	24.9
1992	486 709	5.8	85 959	17.7
1993	265 806	3.1	143 190	53.9
1994	117 077	16.2	20 300	17.3
1995	504 490	7.0	46 384	9.2

[a]Density was calculated using the product of accessible river km for spawning and mean stream width (measured at summer low water levels). Separate values were calculated each year.

1993). In 1994, the year of highest egg density in Catamaran Brook (16.2 eggs·m^{-2}), winter survival was still 1.9 times greater than that in 1995 but similar to survival for the 1992 cohort when egg density was much less (Table 5).

Environmental factors have been suggested as affecting winter survival of salmonids, at various life-stages (e.g., Frenette et al. 1984; Seelbach 1987; Baglinière et al. 1993; Cunjak and Randall 1993; Power et al. 1993; Cunjak 1996; Meyer and Griffith 1997). Gibson and Myers (1988), in examining stock-recruitment data for six rivers in New Brunswick and Newfoundland, found a significant positive relationship between winter discharge and survival of underyearling salmon. For Atlantic salmon in Indian River, Newfoundland, Chadwick (1982) found annual egg-to-fry survival ranged between 22 and 67% and was significantly correlated with winter air temperature and stream discharge. Based on these relations, Chadwick suggested that low streamflow conditions in winter resulted in the freezing of redds. Power (1969) similarly suggested that egg mortality might occur from redd freezing in the salmon rivers of Ungava Bay. Such speculation is intriguing. As noted previously, however, the requisite physical conditions leading to eggs freezing within redds are very complex.

In Catamaran Brook, winter hydrographs (Fig. 2) were analysed to determine if streamflow conditions might explain egg to fry survival. When egg-fry survival was tested against mean winter discharge (Fig. 3A), a weak positive relation (r^2 = 0.173) was found. Unlike the trend for the first 5 winters where egg - fry survival clearly increased as winter streamflow increased, the high mean discharge in 1995–1996 was associated with the lowest survival. Residuals calculated for the regression analysis indicated that the winter of 1995–1996 was an outlier. Indeed, when that winter was excluded from the analysis, discharge explained >90% of the variability in the egg to fry survival, suggesting a strong relation between winter streamflow and egg survival (Fig. 3*a*).

What happened in the winter of 1995–1996 that could account for the extremely poor survival that year? As in 1992, the 1995 spawning cohort deposited about 500 000 eggs (Table 5) over >8 km of the brook. Mean winter discharge in 1995–1996 was high and very similar to that measured in 1990–1991 (Fig. 2) when the best egg survival was measured (Table 5). Air temperature records for the basin indicated a relatively mild winter (Fig. 2).

Catamaran Brook normally experiences a winter characterized by freeze-up in late November, an approximate 4-month period of ice growth, and a spring break-up in March-April (Fig. 2). In 2 of the 6 years shown, however, this typical trend was interrupted by midwinter break-ups: mid-December 1993 and late-January 1996. In both cases, peak discharge values of 6–7 m^3·s^{-1} were in the same range as those that typify the late-spring freshet (3–9 m^3·s^{-1}) but the physical severity of these midwinter events differed markedly. Although no direct, quantitative measures of physical disruption induced by these events were available, an indication of such was derived by comparing the controlling hydrometeorological conditions.

Two useful indices of break-up severity are pre-break-up ice strength (Prowse et al. 1990) and thickness, the latter especially as compared with the pre-break-up flow depth. The thicker an ice cover, the more likely it is to scour the banks and bed and, if of sufficient mechanical strength, to form ice jams. Although records of river-ice thickness are unavailable for the study site, it is possible to estimate pre-break-up values by using temperature-index models for ice growth (Michel 1971) and decay (Bilello 1980). Ice thickness (t_i) can be obtained from

$$t_i = \alpha D_f^{0.5}$$

where is α a coefficient varied to account for conditions of exposure, surface insulation, and subsurface heat flux (mm·°C$^{0.5}$·d$^{0.5}$), and D_f is the accumulated degree-days for mean air temperatures <0°C. Similarly, ice thickness reductions during the pre-break-up period (t_m) is estimated from

$$t_m = \beta D_b$$

where β is an empirical coefficient found by Bilello (1980) to range between 0.004 to 0.01 (m·°C^{-1}·d^{-1}) for northern (>60°N) rivers.

The above two equations were used with the daily air temperature data in Fig. 2 to determine values of pre-break-up ice thickness for the two midwinter events. A value of 14, characteristic of a *"sheltered small river with rapid flow"* (Michel 1971), was employed for α. β was set to 0.004, a value found by Prowse et al. (1989) to be applicable for the Nashwaak River, New Brunswick, which is within 100 km of the Catamaran Brook basin. Dates of freeze-up (beginning of ice growth) were determined from water-temperature records and field observations of ice conditions. In 1993, break-up was preceded by 17 days of ice growth resulting in a pre-break-up thickness of ~11 cm. Calculations of t_m were not included in this calculation recognizing that air temperatures were <–5°C on only 4 of the 17 "growth" days. The

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Fig. 2. Winter hydrometeorological data collected in Catamaran Brook and its basin for the period, 1990–1996. Daily discharge as measured at the hydrometric gauge, river km 9.5; mean winter discharge (Q_{mean}) was measured for the period from 01 November (assumed date of egg deposition) to 31 March (the presumed last day of winter and start of snowmelt/runoff). Cumulative precipitation for snow is measured in water equivalents (mm); rain and snow were measured separately except for January–May 1994, when only total precipitation was recorded.

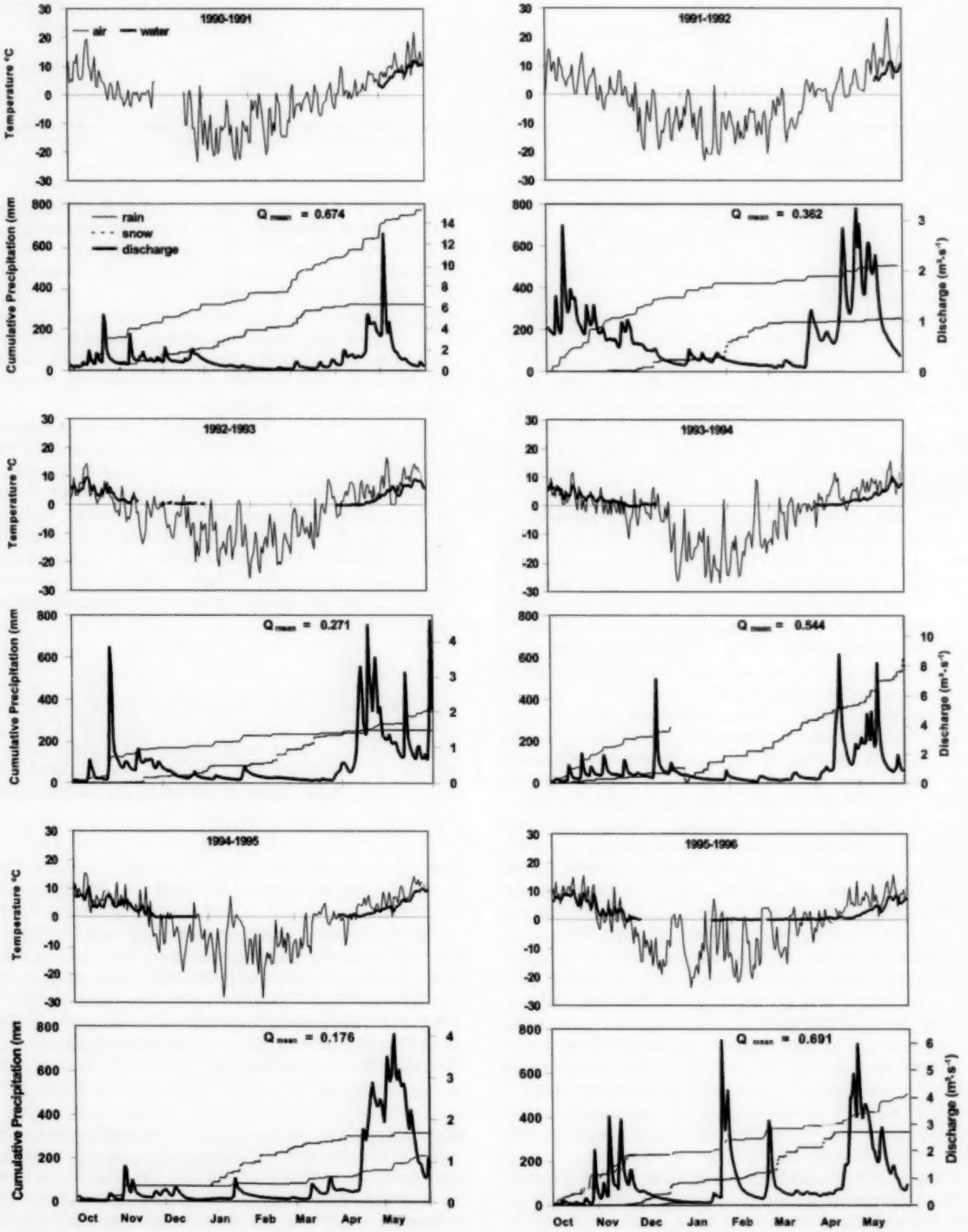

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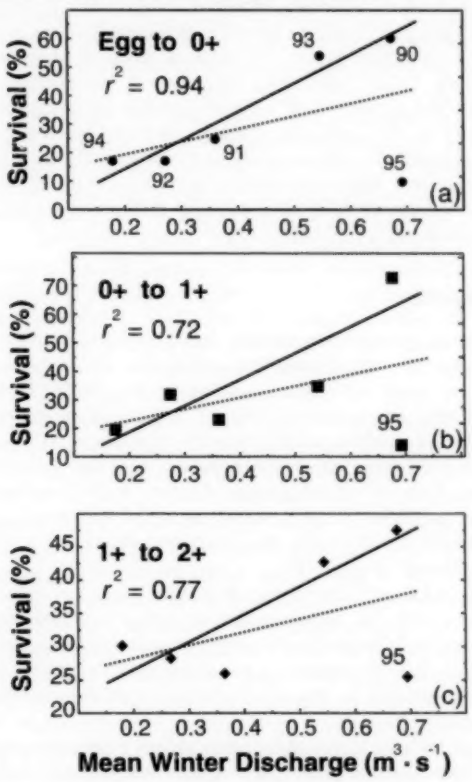
Fig. 3. Linear regression plots of mean winter discharge ($m^3 \cdot s^{-1}$) and survival of different stages of juvenile Atlantic salmon in Catamaran Brook 1990–1996. Solid line is regression excluding winter of 1995–1996; dashed line is regression using data for all six winters. Year values associated with points refer to the start of a particular winter (e.g., 95 refers to the 1995–1996 winter). (*a*) Egg to emergent fry survival (November–June); (*b*) Summer 0+ to summer 1+ survival (1 year interval); (*c*) Summer 1+ to summer 2+ survival (1-year interval). The r^2 values are calculated for regressions excluding the 1995–1996 winter.



potential over-prediction of ice thickness resulting from this, however, is assumed to be offset by increased rates of ice growth when the cover is relatively thin. That is, when <10 cm, t_i increases in direct proportion to D_f rather than its square root (Ashton 1986).

It is unlikely that the relatively thin ice cover of mid-December, 1993, equalling <20% of the flow depth at this time of early winter recession in flows, presented much of an obstacle to the flood wave produced by the rapid runoff. As such, it is unlikely that break-up ice jamming and associated ice scour caused much physical disruption of the channel. In essence, this event was similar to that of an open-water runoff event.

By contrast, the mid-January event of 1996 (Fig. 2) was characterized by a much larger, pre-break-up ice thickness of ~31 cm (t_i = 33 cm; t_m = 2 cm), a result of 55 days of potential ice growth between freeze-up and break-up on January 24, 1996. This large thickness developed, and gradually occupied most of the channel depth, as water levels declined to near-winter minima. One week prior to the increase in flows that immediately preceded break-up, flows were approximately 0.1 $m^3 \cdot s^{-1}$, only 20% of the flow at freeze-up. With this decline in flow and stage, and concomitant growth in ice, it is probable that the pre-break-up ice cover was freeze-bonded over a significant portion of the wetted perimeter (i.e., stream banks and protruding portions of the bed, such as large boulders) that existed at freeze-up.

As for 1993, the 1996 midwinter break-up was initiated by a rain-on-snow event in which rapid development and prevailing meteorological conditions offered little opportunity for the ice sheet to thin or decrease in strength from radiation decay. Hence, it is believed that the thick ice cover that existed on January 24, 1996, would have offered considerable resistance to the downstream passage of the flood wave that peaked at a mean daily flow of 6.1 $m^3 \cdot s^{-1}$ on the day of break-up. The rapidly rising flow and water levels accompanying this flood would have lifted and dislodged the intact ice cover and, given its large relative thickness, would probably have caused severe scour of the bed and banks as it was driven downstream. In general, the hydro-meteorological conditions that characterized the 1996 midwinter event are most typical of dynamic break-up events which are known to produce severe ice jams and to cause maximum disturbance to the fluvial geomorphology of rivers (Scrimgeour and Prowse 1993; Scrimgeour et al. 1994) such as Catamaran Brook. Finally, the limited ice growth and snow accumulation (see Fig. 2) that followed the midwinter (January) 1996 event led to a late-winter *thermal* break-up — one that produced minimal disturbance of the stream channel.

Further support for substrate disturbance in Catamaran Brook during the winter of 1995–1996 was evidenced from Fredle Index (f_i) calculations (Fig. 4). This index was developed by Lotspeich and Everest (1981) to quantify streambed porosity and the reproductive potential of spawning gravel by relating particle sizes to a sorting coefficient, and has been directly linked to salmonid alevin survival. In the spring of 1996, a significant ($p < 0.05$) decrease in substrate quality was measured in the lower reach of Catamaran Brook (Fig. 4) in an area typically used for spawning. By 1997, sediment porosity had still not recovered to levels measured prior to the winter scour event of 1995–1996 (Fig. 4) despite stream discharge peaks of >7 $m^3 \cdot s^{-1}$ measured in the summer of 1996 and in the spring of 1997 (D. Caissie, unpublished data). These data indicate a severe disruption of the substrate and high infiltration of fines during the winter of 1995–1996.

Based on these analyses, we suggest that the combination of mild weather initiating runoff, and the rain-on-snow event of late-January 1996, initiated a mechanical (dynamic) break-up of a significant ice cover in Catamaran Brook. The subsequent increase in river stage and discharge and associated ice scour caused major bedload movement and substrate disturbance. Might the 1995–1996 egg mortality in Catamaran Brook have been due to low winter streamflow (as suggested for other winters), the effect of which was masked by the January break-up event and associated discharge peak? This scenario seems improbable. If the period of the discharge peak was removed from the calculations,

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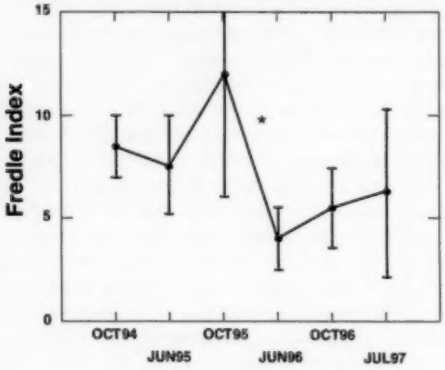
Fig. 4. Seasonal changes in spawning substrate quality in the lower reach of Catamaran Brook, NB as determined by Fredle index estimates (mean ± SD), 1994–1997. Each point is a composite of 2–3 substrate samples (to 20 cm depth) covering 1 m^2 from two spawning sites (see St. Hilaire et al. 1997 for full description of methodology). Asterisk indicates significant difference ($p < 0.05$) between two dates as determined by *a posteriori* Bonferroni test following ANOVA (Systat 1996).



mean winter discharge in 1995–1996 was 0.522 $m^3 \cdot s^{-1}$, still relatively high (Fig. 2) and still an obvious outlier to the discharge-survival regression (Fig. 3).

Interestingly, regression plots of interannual survival for age 0+ to 1+, and for 1+ to 2+ parr were also closely related to, and well explained by, mean winter discharge (Fig. 3*b*,*c*). These results suggest that parr, as well as eggs, were severely affected by low water levels and reduced habitat availability in winter and also by the midwinter break-up event of 1995–1996. This relationship was less expected as the data for parr deal with a 12-month interval and more potential variables (environmental and density-dependent) affecting survival.

The impact of winter discharge on survival, although realized among all life-stages, was particularly devastating on egg survival, perhaps a reflection of the immobility and restrictive niche of this life-stage. The implications for juvenile salmon population dynamics are significant because this stage is the set-point for determining the size of subsequent life-stages and, ultimately, smolt production. For example, the 1996 smolt output from Catamaran Brook (predominantly age-3) was well below average (Cunjak and Therrien 1998; Hardie et al. 1998). Although the number of age-3 pre-smolts (predominant smolt age-class) was certainly affected by the January 1996 break-up, that smolt cohort was the result of the 1992 egg deposition which,albeit high, realized poor egg-0+ survival (Table 5), as a consequence of the low winter discharge (Figs. 2, 3*a*) and reduced habitat availability beneath a very thick ice cover (estimated to be between 42 and 48 cm by the time of April 1993 break-up).

It is important to relate the significance of events, such as the winter 1995–1996 break-up, on salmon populations at various spatial and temporal scales. In the Catamaran Brook catchment, the impact of the midwinter break-up on juvenile salmon survival was similarly realized in three study reaches representing approximately 15 km of stream. The magnitude of the January 1996 event, in terms of discharge, was far less than the 1-in-25 year flood of May, 1991 (Fig. 2), *not* an ice-related flood. That flood had little impact on the salmon population as egg survival was the highest recorded (61.9%, Table 5), and parr abundance and densities in the summer of 1991 were among the highest estimated, in all reaches (Cunjak and Therrien 1996). In the larger branches of the Miramichi, specifically the Little Southwest Miramichi River into which Catamaran Brook drains, the midwinter 1995–1996 break-up had little apparent effect on juvenile salmon densities estimated by electrofishing in the late summer of 1996. D. Moore (Canada, unpublished data) found that parr densities actually increased in index sites relative to previous years. By contrast, a major, dynamic ice break-up in the main river branches of the Miramichi in April 1994 was believed to be responsible for the significant declines in YOY and parr densities in many index sites later that summer (D. Moore, unpublished data). No such break-up, or related impact to salmon survival, was found in Catamaran Brook in 1994; instead, egg and parr survival were quite high (Fig. 3, Table 5).

Summary

The foregoing demonstrates the dynamic physical nature of winter in northern streams and rivers. As was shown in the case study for Catamaran Brook, the effects of winter conditions, particularly discharge and break-up events, on survival of Atlantic salmon can be significant although the nature and magnitude of the impact is complex and dependent on a variety of interrelated factors. Such complexity is further evidence of the dynamic nature of the winter stream environment and of lotic ecosystems in general (e.g., Hynes 1975; Power et al. 1995).

The inherent complexity of stream processes, of which winter is but one important factor, serves to underscore the need for interdisciplinary research in order to understand biological change. Following are some suggestions for future research related to the winter biology and conservation of Atlantic salmon.

There is a need to conduct manipulative field experiments to address the linkages of lipid levels, fish size, and maturity on winter survival. For example, Hutchings (1994) suggested a relation for winter survival, lipids, and maturation costs for brook trout in a Newfoundland stream The enlightening experimental findings by researchers such as Pickering and Pottinger (1988), Metcalfe and Thorpe (1992), Bull et al. (1996), and Gregory and Griffith (1996) need to be field tested for their relevance to what is happening in salmon rivers in Europe and North America.

Can a link be made between "severity" of in-stream habitat, stream morphology, and spatial scale? Is it possible, for example, that at some point along small (first–third order) streams, channel width:depth ratios change to favour winter survival because of less streambed disturbance during spates, reduced probability of dynamic ice break-up, less anchor ice production because overhead canopy reduces radiant heat loss, and because of less freezing to stream bottom due to perching of sheets? By contrast, ice accumulation can be relatively more extensive in larger, wider rivers and disturbance is more likely than in headwaters and tributaries. Might these spatial differences in the probability of winter

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disturbance explain the apparent attempts by Atlantic salmon to spawn as far upstream as possible each year (e.g., Hay 1989; Cunjak, unpublished data)? Interdisciplinary research aimed at comparing egg and juvenile survival for varying stream orders relative to stream morphology and reach-specific hydrology could answer such questions.

Competition for space during winter has long been suggested as a major factor in population regulation in winter (Chapman 1966). Does competition for winter habitats affect juvenile Atlantic salmon populations in rivers? In North America and in Europe many stream species that coexist with Atlantic salmon share similar habitat preferences — i.e., access beneath cobble to boulder-sized substrates. These observations led Cunjak (1988*a*) and Heggenes et al. (1993) to speculate about potential competitors for winter space because habitat availability was more restricted than in summer. Recently, Gregory and Griffith (1996) have quantified aggressive behaviour among YOY salmonids as fish entered concealment habitat at water temperatures between 2 and 6°C in a laboratory setting. That the aggression was primarily initiated by the largest individuals and resulted in displacement of subordinate fishes might explain the smaller size of immigrant YOY Atlantic salmon compared with larger "resident" YOY that remained in the same stream habitat all winter (Cunjak and Randall 1993). Is this evidence of winter competition?

Coincident with the need for further research is the realization that different, and often innovative, approaches to field studies are needed to effectively study the winter behaviour of fishes (e.g., Emmett et al. 1992; Presnyakov and Borisenko 1993) and physical winter phenomena (e.g., Arcone and Delaney 1987). Indeed, the same rigorous environmental conditions to which fishes, such as the Atlantic salmon, have adapted for overwintering often preclude the use of traditional techniques for scientific study and partly explain the dearth of information on the topic. For example, physical habitat measurements associated with freeze-up and anchor ice formation, and the severity of ice break-up in rivers has made field studies logistically difficult during these periods. As a result, most of our knowledge about the effects of ice break-up and formation are based on post-impact assessments. Moreover, these are few in number and have primarily focused on physical impacts. Scientific monitoring around events of such (potential) magnitude and force may require specialized technology as well as different sampling regimens and study designs in order to account for the temporal variance in estimates of population abundance (e.g., Underwood 1991).

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Implications of territory size for the measurement and prediction of salmonid abundance in streams[1]

J.W.A. Grant, S.Ó. Steingrímsson, E.R. Keeley, and R.A. Cunjak

Abstract: Information about territory size is useful for both the measurement and prediction of salmonid abundance. Percent habitat saturation (PHS), the percentage of the stream area occupied by the territories of salmonid fishes, is a better measure of abundance than population density because the former integrates the effects of (*a*) several age-classes or species in a stream, and (*b*) variation in growth rate or sampling date. "Effective density" or "effective PHS," calculated by weighting crude density (no.·m^{-2}) or PHS by the number of organisms in the sampling unit, more accurately reflects density from the organism's point of view than does crude density or PHS. Effective density and PHS of Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick, increased by 0.4 fish per m^2 and 4%, respectively, for each order of magnitude decrease in the area of the sampling unit. Literature data suggested that territory size is inversely related to food abundance and can be used to predict changes in salmonid abundance that accompany changes in food abundance. The allometry of territory size was a better predictor of the decline in density of a cohort of Atlantic salmon in Catamaran Brook than the allometry of metabolic requirements.

Résumé : L'information relative à la taille du territoire est utile tant pour la mesure que pour la prévision de l'abondance des salmonidés. Le pourcentage de saturation de l'habitat, soit le pourcentage de la superficie d'un cours d'eau qui est occupé par les territoires des salmonidés, est une meilleure mesure de l'abondance que la densité de la population parce qu'il intègre les effets (*a*) de la multiplicité des classes d'âge ou des espèces dans le cours d'eau et (*b*) de la variation des taux de croissance ou des dates d'échantillonnage. La « densité effective » ou le « pourcentage effectif de saturation de l'habitat », calculés en pondérant la densité brute (nombre de poissons·m^{-2}) ou le pourcentage de saturation de l'habitat en fonction du nombre d'organismes dans l'unité d'échantillonnage, reflètent plus exactement la densité du point de vue de l'organisme que ne le fait la densité brute ou le pourcentage de saturation de l'habitat. La densité et le pourcentage de saturation de l'habitat effectifs dans le cas du saumon atlantique (*Salmo salar*) du ruisseau Catamaran, au Nouveau-Brunswick, se sont accrus de 0,4 poisson par m^2 et de 4 %, respectivement, pour chaque diminution d'un ordre de grandeur dans la superficie de l'unité d'échantillonnage. Les données tirées de la documentation scientifique laissent entendre que la taille du territoire varie en raison inverse de l'abondance de la nourriture et peut être utilisée pour prévoir les changements dans l'abondance des salmonidés qui accompagnent les changements dans l'abondance de la nourriture. L'allométrie de la taille du territoire était un meilleur facteur de prévision de la baisse de la densité d'une cohorte de saumon atlantique dans le ruisseau Catamaran que l'allométrie des besoins métaboliques.

[Traduit par la Rédaction]

Introduction

The abundance of Atlantic salmon (*Salmo salar*) in fresh water can be usefully studied at any of the nine orders of magnitude of spatial scale that exist within watersheds (Imhof et al. 1996; Folt et al. 1998). For example, information on summer habitat use and preference are best gathered at the level of microhabitat or site (e.g., deGraaf and Bain 1986; Morantz et al. 1987), whereas winter habitat use is best studied at the level of reach or stream (Cunjak 1996). In contrast, action at a watershed level is required to restore salmonid populations in acid stressed environments (Lewis et al. 1996).

Studies of salmonids are most frequently conducted at the site level (~100 m^2, see Imhof et al. 1996), a spatial scale that is too small to address many ecological questions

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J.W.A. Grant[2] and S.Ó. Steingrímsson. Department of Biology, Concordia University, 1455 de Maisonneuve Blvd. West, Montréal, QC H3G 1M8, Canada.
E.R. Keeley. Department of Zoology, The University of British Columbia, 6270 University Blvd., Vancouver, BC V6T 1Z4, Canada.
R.A. Cunjak. Department of Biology and Faculty of Forestry and Environmental Management, University of New Brunswick, Bag Service 45111, Fredericton, NB E3B 6E1, Canada.

[1]Contribution No. 42 of The Catamaran Brook Habitat Research Project.
[2]Author to whom all correspondence should be addressed. e-mail: grant@vax2.concordia.ca

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(Lewis et al. 1996; Armstrong et al. 1998). To rectify this situation, research is increasingly conducted at a variety of larger spatial scales (Cunjak 1996; Imhof et al. 1996; Lewis et al. 1996; Rabeni and Sowa 1996). While this trend is laudable, we believe that questions regarding the mechanisms of competition should often be considered at small spatial scales (see Ray and Hastings 1996).

In this paper, we deliberately take a small-scale approach to the measurement and prediction of the abundance of salmonid fishes in streams. Our basic unit of study is the territory of an individual fish. The study of territories may provide valuable information regarding the habitat, space, and food requirements of individuals with the highest status (sensu Gross 1996) in stream populations (Puckett and Dill 1985; Elliott 1990; Grant 1990). Because defended home ranges (i.e., territories) tend to be smaller than undefended home ranges (Grant et al. 1992), territory size potentially provides information about the minimum spatial requirements of individuals or the maximum density of populations. An allometric territory size relation (e.g., Grant and Kramer 1990; Keeley and Grant 1995) may allow this information to be scaled for individuals of any size in the population, or even among species.

The purpose of our paper is to explore how such a small-scale, space-use approach may provide new insights about the abundance of stream-dwelling salmonids. Specifically, we address how to measure abundance, how spatial scale affects those measurements, how food and (or) space affect abundance, and whether the concept of self-thinning is useful for predicting declines in the abundance of cohorts.

How to measure the abundance of salmonids?

The abundance of a population is usually expressed as population density, the number of organisms per unit area (Krebs 1989; Begon et al. 1996). There are at least two major problems, however, associated with using population density as a general measure of abundance. First, it is difficult to identify, much less count, individuals in modular organisms such as plants. Second, even in unitary organisms (sensu Begon et al. 1996), such as salmonid fishes, individuals within a population often vary in body size. Individuals differing in body size should not necessarily be treated equally in estimates of abundance.

Atlantic salmon are a classic example of a species with indeterminate growth. Juvenile salmon emerge from the gravel weighing about 0.15 g (Randall 1982), leave the stream as smolts weighing about 40 g, and begin returning to the stream to spawn as grilse weighing about 1400 g (Scott and Scott 1988). Even in fresh water, there are usually at least three age-classes of juveniles present in Canadian streams, varying in body length by 6-fold and in body mass by 260-fold (Scott and Scott 1988).

How does one measure abundance for a population of juvenile Atlantic salmon when individuals vary so much in size? For studies of population dynamics, it is important to report population density separately for each age-class (e.g., Elliott 1984; Cunjak and Therrien 1996). But, because different age-classes or species of juvenile salmonids often compete for habitat and food (Symons and Heland 1978; Fausch 1988), strong age-classes often affect the growth and mortality rates of other age-classes or species in the stream (Kennedy and Strange 1986). In some circumstances, therefore, it will be desirable to estimate the total abundance of all age-classes or species in the stream. Summing densities of different age-classes will not be adequate for studies of energy flow or production because a 25 g parr eats more food and occupies more space than a 0.2 g individual.

One can circumvent the problem of individuals differing greatly in size by summing biomass (e.g., $g \cdot m^{-2}$) rather than densities (Krebs 1994). Biomass is used routinely by forestry and fisheries biologists. The major drawback with using biomass is the assumption that two small fish are equivalent to one larger fish of the same mass. Two smaller fish eat more food than one larger fish of equivalent mass because of the allometry of food consumption ($M^{0.73}$), where M is body mass) and metabolic rate ($M^{0.87}$) in salmonid fishes (for a review, see Steingrímsson and Grant 1999). To solve the allometric problem, one can sum the metabolic requirements (e.g., Bohlin et al. 1994) or the food consumption (e.g., Marschall and Crowder 1995) of cohorts in the population. The units of these "allometrically correct" measures, however, are less heuristically appealing than biomass per m^2.

An alternative method for expressing abundance is to estimate the spatial requirements of a population. Some individuals defend feeding territories in virtually all populations of stream-dwelling salmonids (see Titus 1990, for a review). While many factors influence territory size, body size alone explains between 69 and 97% of the variation in territory size (Keeley and Grant 1995; Keeley and McPhail 1998). If territory size is a useful predictor of the space required by a salmonid fish, then we can use the allometric relationship to calculate habitat fullness. Percent habitat saturation (PHS) is the sum of the predicted territory areas of all salmonids in the stream (Grant and Kramer 1990). To calculate PHS, for n cohorts, size classes or species of salmonids in a stream:

$$\mathrm{PHS} = 100 \cdot \sum_{i=1}^{n} D_i \cdot T_i$$

where D_i is the density ($\mathrm{no.} \cdot m^{-2}$) of size class i and T_i is the territory size (m^2) for size-class i (predicted from: $\log_{10}$ territory size = 2.61 $\log_{10}$ fork length (cm) – 2.83; Grant and Kramer 1990). When calculating the PHS for Atlantic salmon in Catamaran Brook, we used the territory size regression specifically for that population: $\log_{10}$ territory size = –3.23 + 3.91 $\log_{10}$ fork length – 0.76 age, where age is 0 for young-of-the-year fish or 1 for older fish (Keeley and Grant 1995). A PHS of 100 means that salmonid fishes fill the surface area of the stream bottom, assuming that territory size is a reasonable estimate of the space required by both territorial and non-territorial individuals. PHS is a convenient measure of salmonid abundance because it gives the fisheries manager an immediate idea of the likelihood that a population is at carrying capacity. In a comparative survey, density dependent population responses were likely when PHS exceeded 27% (Grant and Kramer 1990), presumably because most habitat in a stream is unsuitable for juvenile salmonids. Ideally, one should calibrate the PHS that is

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equivalent to the carrying capacity for each population under study.

We suggest that PHS is a better measure of abundance than density, even when only one age-class is being studied. For example, Steingrímsson (1996; see also Steingrímsson and Grant 1999) counted, from behind a blind, the number of age 0+ salmon in 80, 1-m^2 quadrats of Catamaran Brook, New Brunswick over the 1995 growing season. The average density and PHS for 0+ salmon were 2.2 per m^2 and 16.7%, respectively. While density declined from an average of 4.0 per m^2 in late June to 0.7 per m^2 in late August (Fig. 1*a*; $r = -0.95$, $n = 9$, $P < 0.01$), average PHS showed no marked seasonal trend (Fig. 1*b*; $r = -0.04$, $n = 9$, $P > 0.05$). Hence, measuring only density would have given the false impression that abundance was declining seasonally in Catamaran Brook. In contrast, measuring PHS demonstrated that the decline in population density was just balanced by an increase in the spatial requirements of the surviving, larger individuals. PHS incorporates important variation due to sampling date, size of fish, or growth rates between years that is ignored if population density is used as an index of abundance.

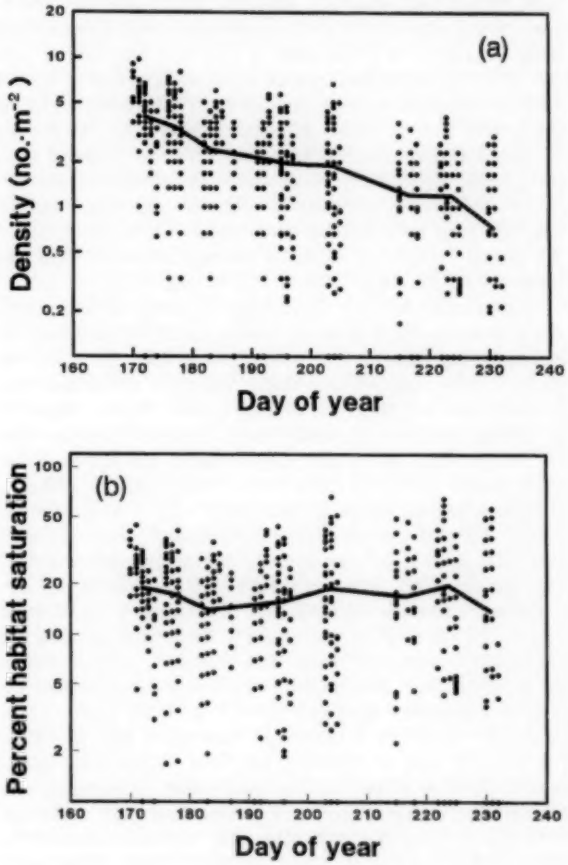
Spatial scale and population abundance

At what spatial scale should population abundance be measured? Operationally, this question can be broadly framed as a problem of optimal "quadrat" size. Quadrat size is an important problem for ecologists only because of spatial heterogeneity in population abundance. If individuals are uniformly distributed in the habitat, then measures of population abundance at all spatial scales will give the same answer.

Optimal quadrat size can be defined either statistically or ecologically (Krebs 1989). The statistical definition is the easier of the two because of its narrower goal: the quadrat size that estimates population density with the greatest precision for a given sampling area, time, or money. High precision requires a low standard error of the mean — i.e., low variance in density between quadrats. Hence, it is often desirable to increase the spatial heterogeneity in density within a quadrat in order to decrease the variance of density between quadrats (Krebs 1989, pp. 64–72). In contrast, there is no single ecological definition of optimal quadrat size, because the optimum will depend upon the goal of the study (see Introduction). Because one of our goals is to evaluate the relative "fullness" of habitats, we will explore how spatial scale influences measures of population abundance.

The standard measure of population abundance for individuals of the same size is the number of organisms per area of habitat. This "crude density" (Smith 1996) is equivalent to the "resource-weighted density" of Lewontin and Levins (1989), when space is the resource. A fundamental problem with crude density is that not all habitat within the sampled area will be suitable for the organism. Hence, a better measure of population density would consider only suitable habitat. But, habitat cannot be dichotomized into completely suitable and completely unsuitable. Instead, habitat suitability will likely be continuously distributed and influenced by population density (Fretwell and Lucas 1970).

Fig. 1. (*a*) Density and (*b*) PHS of young-of-the-year Atlantic salmon counted in 80, 1-m^2 quadrats of Catamaran Brook, during the summer of 1995. Solid lines join the mean values for each of the nine counts. Densities of 0 are placed on the x-axis.



An alternative approach is to express the average density that the organisms in the population actually experience (see Folt et al. 1998). Such an "organism-weighted density" or "effective density" (Lewontin and Levins 1989) is calculated by weighting the crude densities for each sampling unit by the number of organisms in the unit. This weighting scheme is equivalent to using the crude density as a continuous measure of habitat suitability. Crude and effective density are analogous to average and typical group size in the behavioural ecological literature (Jarman 1974). To estimate the "effective density" of a population accurately, the heterogeneity in density within quadrats should be minimized (Lewontin and Levins 1989). Hence, the measure of effective density will continue to increase as quadrat size (i.e., spatial scale) decreases, until the heterogeneity within quadrats is zero. The smallest spatial scale possible is to measure the crude density surrounding each individual in the population. Because of the limitations in using crude density as a measure of salmonid abundance (see previous section), one can also calculate effective PHS: the PHS of a sampling unit weighted by the number of organisms in the unit.

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To illustrate the effects of spatial scale on measures of population abundance, we analyzed Steingrímsson's (1996) data for Catamaran Brook (Fig. 1). He counted 0+ salmon in "flat" habitats (sensu Cunjak et al. 1993) at seven sites for a total of 80, 1-m^2 quadrats. Effective abundance can, therefore, be calculated at three different spatial scales from these data: quadrat (1 m^2), site (80/7 = 11.4 m^2), and habitat type (80 m^2). At the largest spatial scale, effective density and PHS are identical to crude density and PHS, respectively. At the 1- and 11.4-m^2 scales, effective density and PHS are the weighted average crude density and PHS for 80 and 7 sampling units, respectively. As spatial scale increased from 1 to 80 m^2, the average estimate of effective population density over the nine time periods decreased by 28%, from 2.9 to 2.1 per m^2 (Fig. 2*a*), whereas average effective PHS decreased by 32%, from 24.5 to 16.7% (Fig. 2*b*).

To determine whether the patterns observed in Steingrímsson's data also occur at larger spatial scales, we analyzed the electrofishing data for Catamaran Brook from 1991 to 1996 (R.A. Cunjak, unpublished data). Effective abundance can be calculated for each year at four spatial scales (Cunjak et al. 1993): site (n = 20, mean area = 106 m^2), habitat type (i.e., flats, runs, riffles and pools) within reaches (n = 10, mean area = 206 m^2), reach (n = 3, mean area = 780 m^2), and the total area sampled (mean area = 2337 m^2), approximately 2.2% of the stream area. As spatial scale increased from 106 to 2337 m^2, the average effective population density decreased by 34% from 1.50 to 0.99 salmon per m^2, whereas the average effective PHS decreased by 26.2% from 21.4 to 15.8% (Fig. 3). To quantify these relationships, we calculated least-square regressions for each year and then the average slope and intercept of these six regressions: effective population density (no.·m^{-2} ± 95% CL) = 2.24 (± 0.75) – 0.367 (± 0.185) $\log_{10}$ area (m^2); effective PHS (% ± 95% CL) = 30.1 (± 7.4) – 4.19 (± 1.33) $\log_{10}$ area (m^2). The slopes of the least-square regressions for Steingrímsson's data were very similar, and well within the 95% CL for the electrofishing data (effective density = 2.91 – 0.413 $\log_{10}$ area; effective PHS = 24.6 – 4.06 $\log_{10}$ area). The similarity in the slopes from the two data sets suggests a consistent decline in effective salmonid abundance in Catamaran Brook over 3.5 orders of magnitude of spatial scale. For an increase in spatial scale of one order of magnitude, effective population density declines by about 0.4 fish per m^2, whereas effective PHS declines by about 4%.

We were not expecting the intercepts of the two data sets to be similar, because Steingrímsson sampled only one of four habitat types in one of three reaches in one of six years. Nevertheless, the apparent differences in the intercepts are interesting. Population density appeared to be higher in Steingrímsson's data than in the complete brook (compare open circles to solid circles in Fig. 3), whereas PHS showed the opposite trend (compare open triangles to solid triangles in Fig. 3). This apparently contradictory result occurred because Steingrímsson studied only flats, ideal habitat for age 0+ salmon but not for age 1+ or 2+ parr. Flat habitats have high average densities but low average PHS.

Spatial scale can clearly have a large influence on our perception of population abundance (e.g., Fig. 3), even when crude abundance does not change. Because population

Fig. 2. (*a*) Effective density and (*b*) effective PHS from Fig. 1, calculated nine times over the summer at three different spatial scales: 80 m^2 (●), 11.4 m^2 (■), and 1 m^2 (▲).

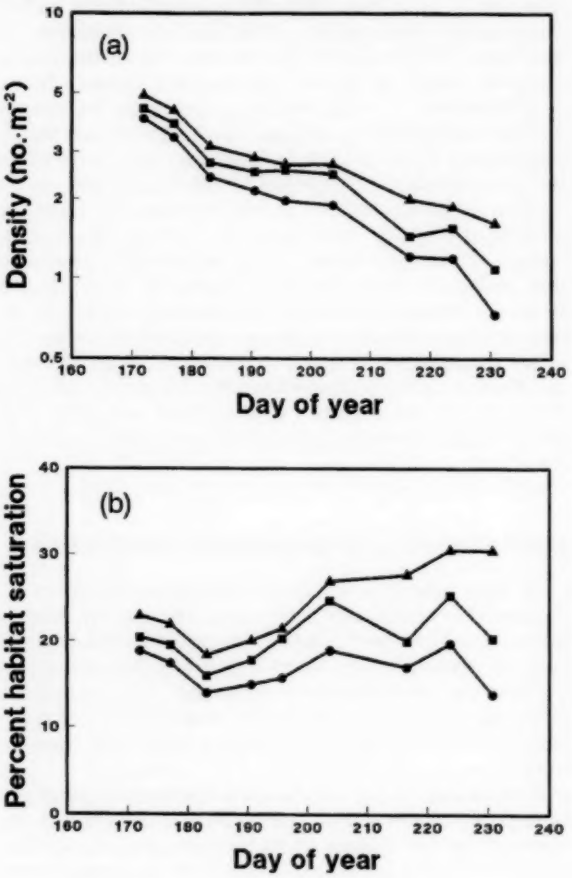
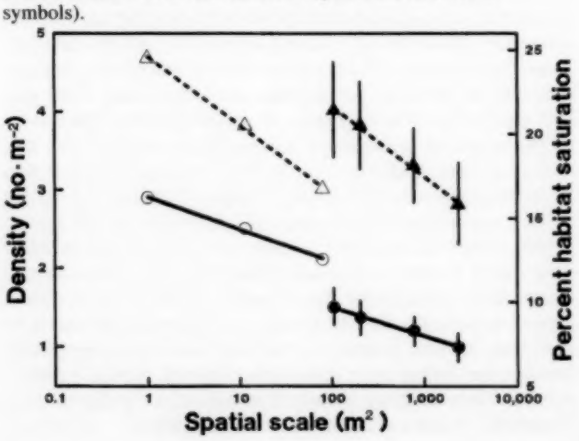


Fig. 3. Average effective density (●, ○) and PHS (▲, △) of juvenile Atlantic salmon at three spatial scales in 1995 (i.e., Fig. 2; open symbols) and from electrofishing data of Catamaran Brook in 1991–96 at four different spatial scales (closed symbols).



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density is most commonly estimated by electrofishing sites of about 100 m^2, the effective abundance that salmonids actually experience will often be underestimated. Population abundance will continue to be measured at a variety of spatial scales, so it would be useful to derive a general version of Fig. 3 to facilitate comparisons of data measured at a variety of spatial scales. In the absence of a general relationship between spatial scale and effective population abundance, spatial scale should be included as a covariate in any comparative analyses of salmonid abundance. For example, Grant and Kramer (1990) used PHS to predict the occurrence of density dependent population response. Presumably, this relationship would be even stronger if some of the noise in the PHS data was removed by adding spatial scale as a covariate.

Food, space, and salmonid abundance

Density dependent growth, mortality, and emigration have been widely reported in stream salmonid populations (Grant and Kramer 1990), indicating that competition is often intense. Because of the occurrence of feeding territories, food and (or) space have long been implicated as the causes of these density dependent responses (Chapman 1966; Allen 1969). But, how food abundance and territory size interact to affect density has not been clearly or quantitatively described. We can imagine four possible scenarios.

The food hypothesis predicts that salmonid abundance will be directly proportional to food abundance (i.e., a slope of 1.0). Hence, a doubling or halving of food abundance would cause a doubling or halving of salmonid abundance (e.g., PHS or biomass). The space hypothesis assumes that minimum territory size is inflexible and predicts a maximum population density (e.g., Allen 1969). The space-equals-food hypothesis assumes that population density is set by both food abundance and territory size. In this scenario, fish vary the size of their territory to maintain a constant supply of food on their territory, so that territory size is just the proximate mechanism for achieving the food hypothesis (e.g., McFadden 1969; Marschall and Crowder 1995). Hence, territory area is predicted to be inversely proportional to food abundance (i.e., a slope of –1.0), and salmonid abundance is predicted to be directly proportional to food abundance (i.e., a slope of 1.0). The food-and-space hypothesis also assumes that both food abundance and territory size affect salmonid abundance. While food abundance has an inverse effect on territory size, which in turn affects population density, no particular assumptions are made about the quantitative relationship between food abundance and territory size (e.g., Chapman 1966).

To test among the four scenarios, we searched the literature for papers that manipulated or measured food abundance while monitoring either territory size or the abundance of salmonids. We used PHS as our measure of abundance whenever possible; otherwise we used biomass or population density (the latter only when fish size did not change within a study). Thus, all measures of abundance were corrected for fish size. Measures of food abundance varied in quality; in decreasing order of quality they included average daily ration in experimental studies, the abundance of drift, or the biomass of benthic invertebrates. For each study, we calculated mean territory size, food abundance and salmonid abundance and then expressed any changes in these variables as multiples of the mean.

Only two studies (Slaney and Northcote 1974; Dill et al. 1981) measured territory size while presenting food in a manner that simulates natural drift (for a review, see Grant and Noakes 1987). Territory size varied inversely with food abundance (Fig. 4*a*). Therefore, we can reject the space hypothesis, which assumes territory size is inflexible. We can also reject the space-equals-food hypothesis because territory size changed much less than one would expect if fish were maintaining a constant supply of food on their territories (Fig. 4*a*); the observed slope was significantly shallower than the predicted slope of –1.0, assuming that food abundance is directly proportional to territory area. If food abundance is directly proportional to territory diameter rather than territory area (see Grant and Noakes 1987), then the difference between the slopes is even greater.

That territory size changes inversely with increases in food abundance is consistent with models of optimal territory size (Schoener 1983). It was surprising, however, how little territory size actually changed. Salmonids typically occupy contiguous territories and may not be "free" to choose the size of their territory. Salmonid territories may be compressed below their non-contiguous optimum by the pressure exerted by their territorial neighbours (Hixon 1980; Grant 1997).

We found only three studies that manipulated food abundance and measured the equilibrium abundance of salmonids. We were initially very cautious about using observational data because of the potential confounding effects of top-down control of food abundance (e.g., Bowlby and Roff 1986). Stream fertilization studies were categorized as observational because both food and salmonid abundance were dependent variables. Because the two types of data gave similar results (ANCOVA, $P = 0.97$), however, we combined both into one analysis. Salmonid abundance increased significantly with food abundance, but the slope of the relationship was significantly less than 1.0 (Fig. 4*b*). The relationship changed little when the single low point in Fig. 4*b* was deleted from the analysis (e.g., slope = 0.51 ± 0.22, $r = 0.77$, $P < 0.001$). Therefore, we can reject the food hypothesis.

To test the food-and-space hypothesis, we overlaid the inverse of the territory area versus food abundance regression (Fig. 4*a*) on top of the data in Fig. 4*b*. For example, a doubling of food causes territories to shrink to 0.76 of their initial size, predicting an increase in salmonid abundance to 1.32 times its initial value. Changes in salmonid abundance were almost perfectly predicted by the inverse of the territory size versus food abundance regression (Fig. 4*b*). These data support the food-and-space hypothesis and suggest that changes in food abundance affect salmonid abundance, but only after passing through the "filter" of territory size.

We believe Fig. 4*b* has important management implications. First, both regressions can be used to predict the response of salmonid populations to changes in food abundance. Second, these data would seem to suggest that increasing the productivity of a stream will have relatively little effect on salmonid abundance. For example, doubling the productivity of a stream would only increase juvenile

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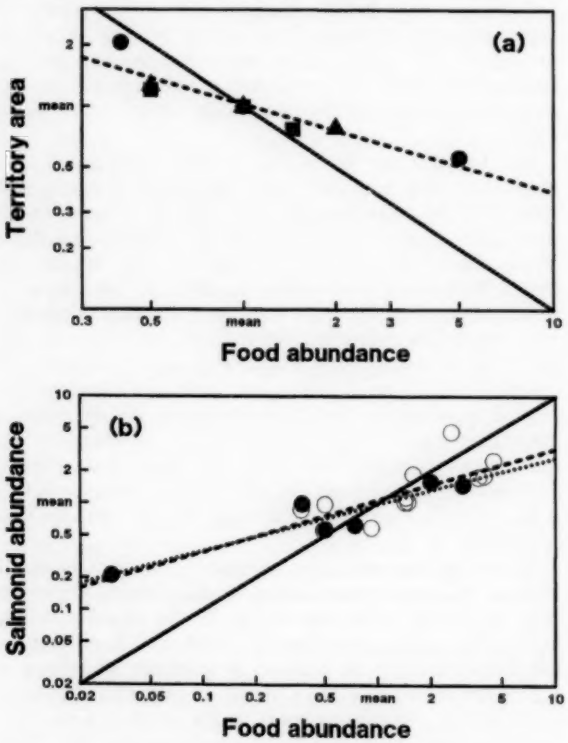
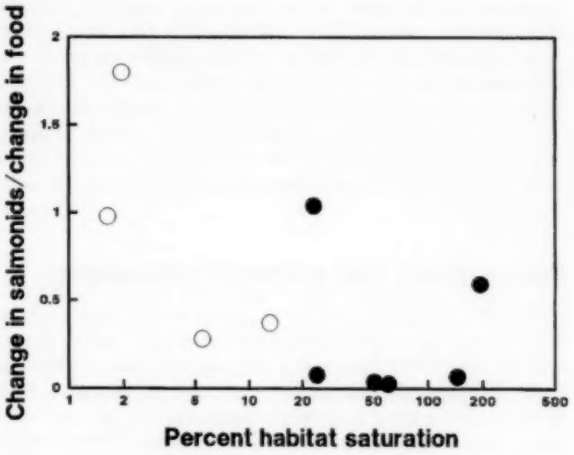
Fig. 4. (*a*) Influence of changes in food abundance (multiples of the mean) on territory size (multiples of the mean) (● = experiment 2, Slaney and Northcote 1974; ▲ = field data from Dill et al. 1981; ■ = laboratory data from Dill et al. 1981). The dashed line is the least squares regression: $\log_{10}$ territory size (± 95% CL) = 0.0108 (± 0.0490) – 0.434 (± 0.151) $\log_{10}$ food abundance (r = –0.93, n = 9, $P < 0.001$). The solid line is the predicted territory size if fish defend a constant amount of food, assuming food abundance is directly proportional to territory area. (*b*) Influence of changes in food abundance (multiples of the mean) on salmonid abundance (multiples of the mean) (● = experimental studies: Slaney and Northcote 1974; Mesick 1988; Keeley 1998) (○ = observational data: Ellis and Gowing 1957; Warren et al. 1964; Murphy et al. 1981; Slaney and Ward 1993; Slaney et al. 1994; Toth et al. 1996; Toth et al. 1997). The dashed line is the least squares regression: $\log_{10}$ salmonid abundance (± 95% CL) = 0.487 (± 0.149) $\log_{10}$ food abundance – 0.0281 (± 0.0739) (r = 0.85, n = 20, $P < 0.0001$). The solid line is the one-to-one line and the dotted line is the inverse of the territory size regression in Fig. 4*a* (i.e., $\log_{10}$ salmonid abundance = 0.434 $\log_{10}$ food abundance – 0.0108).



abundance by 1.32 times, whereas doubling the amount of juvenile habitat, perhaps by removing an unnatural barrier to upstream migration, would presumably double juvenile abundance. While the relationships in Fig. 4 are strong, the data are limited and of variable quality. Hence, we encourage future studies to quantify the relationship between food and salmonid abundance more rigorously in order to test these ideas further.

Fig. 5. Percent change in salmonid abundance/percent change in food abundance, for each of 10 studies in Fig. 4*b*, decreased with increasing PHS (r = –0.62, n = 10, P = 0.054). For each study, PHS was calculated for the lower of two treatments or the mean of three treatments. ○ represent stream fertilization studies.



The prospects for stream fertilization are not quite so bleak as depicted in Fig. 4, because the response of salmonids to changes in food abundance also seem to depend on habitat saturation (Fig. 5). The fertilization of four streams increased the abundance of benthic invertebrates by an impressive average of 219% (Slaney and Ward 1993; Slaney et al. 1994; Toth et al. 1996, 1997). The two streams with the greatest response in salmonid abundance had the lowest initial PHS values of 1.7 and 2% (Toth et al. 1996, 1997). These data suggest that stream fertilization will only be useful in nutrient-poor streams with low initial salmonid abundance. Most of the increase in salmonid abundance resulting from fertilization was caused by an increase in growth rate rather than an increase in population density. Increased growth rate can be beneficial for fisheries managers if it increases overwinter survival of juveniles (e.g., Hunt 1969; Holtby 1988) or reduces mean smolt age (Hutchings and Jones 1998), and hence, increases smolt production (e.g., Slaney and Ward 1993). Unfortunately, increasing juvenile growth rate can also be detrimental by causing a higher proportion of sexually mature male parr or grilse in Atlantic salmon (Hutchings and Jones 1998; Marschall et al. 1998; Metcalfe 1998).

If the food-and-space hypothesis is correct, it suggests that territory size is the proximate factor that limits salmonid abundance. Hence, any environmental factor that reduces territory size should increase population density. Kalleberg (1958) increased the visual isolation of salmon parr, causing territory size to decrease by 51%, presumably because of an increase in the costs of territory defence (see Eason and Stamps 1992). An experimental test of this hypothesis is needed. When Kalleberg increased current velocity from 18 to 29 $cm \cdot s^{-1}$, population density increased by 12%, also presumably because of an increase in the costs of territory defence. Of the two factors, visual isolation had a greater effect on salmonid abundance and would seem to be easier

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to manipulate in the field. Neither manipulation is recommended, however, without first determining their effects on growth rate.

Self-thinning and salmonid abundance

What determines the abundance of a cohort is a separate but related issue to those of the previous section. Metabolic rate across species typically increases as $M^{0.75}$ (Peters 1983). If energy availability does not change with body size, then the "energetic equivalence hypothesis" (Bohlin et al. 1994) predicts that the density of species should scale to $M^{-0.75}$. Across species correlations between density and body mass are often consistent with the predicted slope of –0.75 (Peters and Wassenberg 1983; Nee et al. 1991).

Because of within population variation in body size, we might expect to see the same inverse relation between density and body mass within cohorts of juvenile salmonids. If such declines in density are caused by competition as the individuals within the cohort grow, then the process can be called self-thinning (Lonsdale 1990). In salmonid populations, food consumption and metabolic rate scale to body mass with an average exponent of 0.73 and 0.87, respectively (Steingrímsson and Grant 1999). Thus, the energetic equivalence hypothesis predicts self-thinning slopes of –0.73 or –0.87 for salmonid fishes.

Competition for space could also provide a mechanism for self-thinning. In an interspecific analysis, territory size increased as $M^{0.86}$ (Grant and Kramer 1990). Subsequent studies have shown that allometric territory size relationships differ between species or studies with slopes that vary between 0.82 and 1.12 (Keeley and Grant 1995; Keeley and McPhail 1998). If territory size limits population density directly (e.g., Elliott 1990) or simply predicts spatial requirements of both territorial and non-territorial fish, then the space hypothesis predicts a self-thinning line with a slope between –0.82 and –1.12.

Distinguishing between the space and energetic equivalence hypotheses, which are not necessarily mutually exclusive, will be difficult given the similarity of their predictions. For example, seven of the nine tests of these hypotheses were consistent with the predictions of both (Table 1). Only Elliott (1993) rejected the space hypothesis, whereas only Steingrímsson and Grant (1999) rejected the energetic equivalence hypothesis.

In reality, the two hypotheses may be more different than they first appear because of different underlying assumptions. Existing tests of the energetic equivalence hypothesis have assumed a constant food supply over time and body sizes (Begon et al. 1986; Bohlin et al. 1994). In contrast, the space hypothesis assumes that changes in food abundance are incorporated into the allometric, territory-size relationship. Juvenile Atlantic salmon are size selective foragers so that prey size increases with body size (Keeley and Grant 1997). The percentage of organisms in the drift that are of an edible size was about 90% for salmon less than 2 g, but decreased rapidly with increasing body mass (Fig. 6). This decline in the number of prey available with increasing body size is only partly compensated by larger fish eating larger prey. Because the prey available in Catamaran Brook are small (Keeley and Grant 1997), the biomass of prey available to Atlantic salmon decreases with increasing body size. Seasonal changes in the drift pose an even bigger challenge to the assumption of constant food availability. The abundance of drift in streams often peaks in the late spring or early summer and declines over the growing season (O'Hop and Wallace 1983; Allan 1987; Keeley and Grant 1997). The energetic equivalence hypothesis can be modified to incorporate linear changes in food abundance. If metabolic rate scales as M^b and food abundance scales as M^a, then the modified self-thinning slope is M^{-b+a} (see Begon et al. 1986; Bohlin et al. 1994). Once the energetic equivalence hypothesis is modified to incorporate changes in food abundance with body mass, the two hypotheses may make quite different predictions.

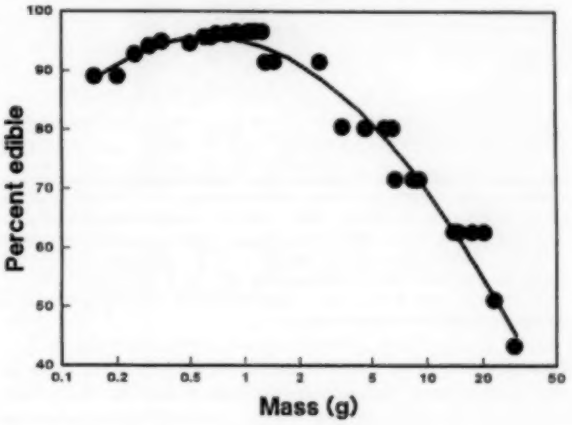

Fig. 6. Percentage of the organisms in the drift that are of an edible size in relation to body mass for juvenile Atlantic salmon in Catamaran Brook (Percent = 95.05 – 7.00 $\log_{10}$ Mass – 18.08 [$\log_{10}$ Mass]^2). Each datum is the predicted value for each of 46 fish based on allometric relationships of minimum and maximum prey length and the length distribution of organisms captured in drift nets in Catamaran Brook (see Keeley and Grant 1997).

Steingrímsson and Grant (1999) took advantage of seasonal changes in food abundance to test the predictions of the two hypotheses. The abundance of drift in Catamaran Brook declined by an average of 94% over the growing season, from 0.34 mg dry weight per 20-min drift sample in mid June to 0.021 mg in mid August. Hence, food for young-of-the-year salmon was proportional to $M^{-2.21}$. The predicted self-thinning slope of the corrected energetic equivalence hypothesis was –3.08 (i.e., $-\beta+\alpha = -0.87 - 2.21 = -3.08$). In contrast, the space hypothesis, specifically for Atlantic salmon in Catamaran Brook, predicted a self-thinning slope of –1.12 (Keeley and Grant 1995). The observed self-thinning slope of –1.16 rejected both the uncorrected and corrected predictions of the energetic equivalence hypothesis, but supported the space hypothesis (Table 1).

Steingrímsson and Grant's (1999) analysis does not mean that self-thinning in Catamaran Brook is not affected by food density. Juvenile salmon in Catamaran Brook increase their territories as if they are trying to maintain a maximum daily ration of food flowing over their territory (Keeley and Grant 1995; also see Keeley and McPhail 1998). How can

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Table 1. "Self-thinning" slopes for stream-dwelling salmonids.

Species	Slope (95% CI)	SH[a]		EEH[b]		Reference
		GEN	SS	MR	FC	
Salmo trutta	–0.74 (–0.71, –0.77)	–	–	–	+	Elliott 1993
	–0.89 (–0.51, –1.27)	+	+	+	+	Bohlin et al. 1994
	–0.94 (–0.71, –1.17)	+	+	+	+	Bohlin et al. 1994
Various	–0.78 (–0.58, –0.98)	+	na	+	+	Grant 1993
	–0.70 (–0.21, –1.20)	+	na	+	+	Dunham and Vinyard 1997
S. salar	–1.07 (–0.84, –1.30)	+	+	+	–	Bohlin et al. 1994
	–0.91 (–0.44, –1.38)	+	+	+	+	Egglishaw and Shackley in Bohlin et al. 1994
Salvelinus fontinalis	–1.16 (–0.90, –1.42)	–	+	–	–	Steingrímsson and Grant (1999)
	–0.88 (–0.16, –1.60)	+	+	+	+	Trépanier and Rodríguez[c]

[a]SH = space hypothesis. GEN = predicted slope of –0.86 from an interspecific regression (Grant and Kramer 1990). SS = predicted slope of –0.82 and –0.99 for brown trout (Elliott 1990), –1.12 for Atlantic salmon (Keeley and Grant 1995), and –0.82 for brook trout (Grant and Kramer 1990). + = predicted slope is within 95% CI of observed slope; – = predicted slope outside of 95% CI of observed slope; na = not applicable.

[b]EEH = energetic equivalence hypothesis. MR = predicted slope of –0.87 based on the allometry of metabolic rate; FC = predicted slope of –0.73 based on the allometry of food consumption (Steingrímsson and Grant 1999).

[c]S. Trépanier and M. Rodríguez, unpublished data. Département de biologie et des sciences de la santé, Université du Québec à Rimouski, CP 3300, Rimouski, Québec, Canada G5L 3A1.

they do this given the 94% decline in drift over the season? As the parr grow and increase the size of their territory, they also move to faster, deeper water. All three factors increase the number of potential prey that fish encounter over their territories (see Hughes and Dill 1990). These data suggest that self-thinning slopes will be steeper (i.e., more negative) in shallow, low-velocity habitats that experience a greater seasonal decline in drift. Steingrímsson and Grant (1999) observed just such a correlation, presumably because fish leave these sites as they grow larger.

The concept of self-thinning will always be more complicated to apply to mobile animals than to sedentary plants. First, it is difficult to know whether animals are experiencing food- or space-related competition at all. There is no easy way of distinguishing between cohorts that are truly self-thinning and those experiencing density-independent growth and mortality (see Armstrong 1997; Steingrímsson and Grant 1999). Ideally, a density-body mass relation should only be called self-thinning if density dependent competition is occurring in that population. Some of the variation in the "self-thinning" slopes reported by Bohlin et al. (1994) and Dunham and Vinyard (1997) likely result from including populations that are not experiencing density dependent competition. Given the difficulty in documenting the occurrence of density dependence, a simple rule-of-thumb might be to reserve the term self-thinning for cases when PHS, preferably effective PHS measured at a small spatial scale, is greater than or equal to 27%, the abundance when density dependent competition is apparent (see Grant and Kramer 1990).

Second, the general self-thinning slope predicted by the energetic equivalence hypothesis may not be broadly applicable because of the failure of the assumption of constant food availability across body sizes. Powerful tests of the energetic equivalence hypothesis will, therefore, require monitoring size-dependent changes in food abundance for each study. Third, size-dependent changes in habitat preference will affect the self-thinning slope in different habitat types (Armstrong 1997; Steingrímsson and Grant 1999). Rather than being a shortcoming, Trépanier's (1997) study suggests self-thinning parameters can be used to determine habitat suitability. The allometry of space use will incorporate much of this variation in size-dependent changes in food abundance or habitat use. The generality of the space hypothesis, however, will depend on whether allometric territory size regressions can be broadly applied for a species or have to be described for each specific population under study. The usefulness of the self-thinning concept for salmonid ecologists will ultimately depend on its ability to generate novel, powerful predictions.

Conclusions

We believe a small-scale approach can provide new insights into the ecology of stream-dwelling salmonids that will complement studies at larger spatial scales. Quantifying territory size appears to be a useful starting point for measuring the abundance of salmonids in streams. Because of spatial heterogeneity, our perception of salmonid abundance from the organism's point of view increases as the spatial scale at which the abundance is measured decreases. Information about territory size is also useful in predicting changes in the abundance of cohorts over time and the response of populations to changes in food abundance. Future research should test the hypothesis that density dependent processes will likely be easier to detect as the spatial scale of the study decreases.

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Juvenile production variation in salmonids: population dynamics, habitat, and the role of spatial relationships

John F. Kocik and C. Paola Ferreri

Abstract: Anadromous Atlantic salmon (*Salmo salar*) exhibit a complex life history that requires the use of habitats that span several different temporal and spatial scales. While fisheries scientists have investigated the various elements of habitat and how they affect Atlantic salmon growth and survival, these studies typically focus on requisite requirements for a single life history stage. Current advances in our understanding of salmonid populations in lotic systems indicates that ignoring the spatial positioning of different habitats and dispersal capabilities of fish between them may affect estimates of habitat quality and production of juvenile Atlantic salmon. Using the concepts of juxtaposition and interspersion, we hypothesize that discrete functional habitat units (FHU) occur within river systems and that the spatial structure of FHU affects fish production. We present a method to delineate FHU using habitat maps, fish ecology, and spatial habitat characteristics. Utilizing a simulation model, we illustrate how modeling FHU structure of spawning and rearing habitat in a river system can improve our understanding of juvenile Atlantic salmon production dynamics. The FHU concept allows a flexible approach to more comprehensive analyses of the impacts of habitat alterations, seasonal habitat shifts, and spatial ecology of salmonids at various scales.

Résumé : Le saumon de l'Atlantique (*Salmo salar*) anadrome a un cycle vital complexe dans lequel l'espèce utilise des habitats qui s'inscrivent dans plusieurs échelles temporelles et spatiales. Bien que les halieutes aient étudié les divers éléments de l'habitat et les façons dont ils influent sur la croissance et la survie du saumon atlantique, ces études se concentrent typiquement sur les exigences du saumon en matière d'habitat durant un seul stade du cycle vital. Les progrès récents dans notre connaissance des populations de salmonidés dans les systèmes lotiques montrent que le fait d'ignorer le positionnement spatial des différents habitats et les capacités de dispersion des poissons d'un habitat à l'autre peut fausser les estimations de la qualité de l'habitat et de la production de saumon atlantique juvénile. À partir des concepts de juxtaposition et d'intercalation, nous formulons l'hypothèse que des unités fonctionnelles discrètes d'habitat sont présentes dans les systèmes fluviaux et que la structure spatiale de ces unités influe sur la production de poisson. Nous présentons une méthode permettant de délimiter les unités fonctionnelles d'habitat utilisant des cartes d'habitat, l'écologie du poisson et les caractéristiques spatiales des habitats. Au moyen d'un modèle de simulation, nous montrons comment la modélisation de la structure des unités fonctionnelles d'habitat des frayères et des alevinières dans un système fluvial peut accroître notre compréhension de la dynamique de la production des saumons atlantiques juvéniles. Le concept d'unités fonctionnelles d'habitat nous permet de réaliser avec souplesse des analyses plus détaillées des impacts des altérations des habitats, des changements saisonniers dans les habitats et de l'écologie spatiale des salmonidés à diverses échelles.

[Traduit par la Rédaction]

Introduction

The conservation and restoration of Atlantic salmon (*Salmo salar*) populations in large river systems is an important task facing many fishery managers (Anonymous 1996). One crucial step towards achieving these goals is to optimize the numbers and quality of smolts produced by a spawning population in a river (Armstrong et al. 1998). To achieve optimal smolt production in streams, fishery managers may choose to manage their riverine habitat; this management may take the form of habitat protection, restoration, or enhancement. However, defining quantitative links between fish habitat and fish population dynamics has been difficult due to gaps in our understanding as to what constitutes habitat for a species and the appropriate scale at which habitat should be defined (Fausch and Young 1995; Grossman et al. 1995; Schlosser 1995; Hayes et al. 1996; Armstrong et al. 1998).

Anadromous Atlantic salmon exhibit a complex life history that requires the use of many different habitats that span many temporal and spatial scales. The environmental requirements of Atlantic salmon during their riverine life stages have been extensively studied and summarized (e.g., Bley 1987; Mills 1989; Shearer 1992; Gibson 1993; Gibson and Cutting 1993; Stanley and Trial 1995). Our review of

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J.F. Kocik.[1] NOAA Fisheries, Northeast Fisheries Science Center, 166 Water St. Woods Hole, MA 02543-1097, U.S.A. **C.P. Ferreri.** School of Forest Resources, 207 Ferguson Bldg., Pennsylvania State University, University Park, PA 16802-4301, U.S.A.

[1]Author to whom all correspondence should be addressed. e-mail: jkocik@whsun1.wh.whoi.edu

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this literature indicated that one aspect is clearly missing from the research on Atlantic salmon habitat use and preference — how the spatial relationships of different habitats for each life stage or season affects overall freshwater production of Atlantic salmon. We found that most of the salmonid literature focuses on specific habitat requirements for a particular life stage or season. There has been relatively little integration of this information across temporal and spatial scales as it relates to population dynamics. Recent studies in riverine systems indicate that habitat complementation (i.e., the spatial proximity of different nonsubstitutable resources) can be a critical factor determining the population size and persistence of fish populations (Scheimer et al. 1991; Dunning et al. 1992; Schlosser 1995). In addition, recent work on salmonid movements in streams has challenged the restricted movement paradigm that has driven analyses of salmonid habitat and population dynamics (Gowan et al. 1994). In combination, these two advances highlight the need to understand the role of the spatial arrangement of different habitat types necessary for fish production in streams. Our goal is to demonstrate that integrating recent advances in spatial habitat analysis with our improved understanding of salmonid movement in streams can facilitate selection of the appropriate scale for evaluating pre-smolt production of Atlantic salmon in streams and lead to better predictions of variability in that production.

Natural units of scale: effects of habitat spacing and fish movement

To determine the appropriate scale at which to study a population segment, it is important to not only identify all of the habitat elements necessary to support every life history stage but also to examine how organisms move between these elements. In this century, wildlife ecology has intensively examined the importance of the spatial aspects of habitat. The work of Leopold (1933) introduced the concepts of habitat interspersion (degree of intermixing of discrete habitat types) and juxtaposition (relative location of discrete habitat types) to emphasize the importance of the spatial aspects of habitat. Over time, it has become a prevailing tenet of wildlife management that the overall suitability and productive capacity of habitat is determined by not only the quality and quantity of habitat for each life stage but also by the spatial relationship of these habitats (Thomas et al. 1979). Equally important is the realization that increased habitat heterogeneity favors edge species, while homogeneous habitat structure increases production of interior species (Thomas et al. 1979; Pearson et al. 1996). Wildlife management has not only embraced the importance of the spatial arrangement of habitat but has successfully used this information in routine management efforts to protect, restore, and enhance wildlife habitat and increase wildlife production (Thomas et al. 1979).

The importance of the spatial elements of habitat analyses were also identified early in fisheries ecology (Chapman 1966). However, the linkage between spatial analysis and fish population dynamics has recently gone through major theoretical advances (Fausch and Young 1995; Grossman et al. 1995; Schlosser 1995; Schlosser and Angermeier 1995). These studies advance the hypothesis that the spatial arrangements of habitat components is important in riverine systems and can give rise to markedly different fish population dynamics at a stream reach level and at larger mesohabitat scales (Grossman et al. 1995; Schlosser 1995). We believe that this hypothesis is well supported for salmonid populations. For example, higher salmonid growth rates occur in stream segments where adequate cover is in close proximity to an abundant food supply; conversely, production is lower in reaches where these two resources are widely separated (White 1991). These relationships likely exist at scales beyond the mesohabitat level because juvenile salmonids utilize different habitats at different life history stages and during different seasons (Symons and Heland 1978; Kennedy and Strange 1986; Cunjak 1988; Heggenes 1991; Heggenes and Borgstrom 1991; Kocik and Taylor 1995, 1996). While these shifts are well documented, population models that attempt to integrate spatial habitat differences are rare (cf. Fausch et al. 1988). A comprehensive model that does integrate these elements, SALMOD (Bartholow et al. 1993; Williamson et al. 1993), has not gained the widespread use of other habitat models such as the Instream Flow Incremental Methodology (Fausch et al. 1988).

The reasons for limited management-level utilization of spatial habitat analyses are elusive but seem related to the complexity of mapping entire river systems (Fausch et al. 1988) and a predominant notion that movement of stream fish was very limited (Gerking 1959; Bachman 1984). Recent technological advances in computer modeling and particularly Geographic Information Systems (GIS) technology are creating more accessible spatial databases and removing many of the analytical barriers that made comprehensive basinwide habitat assessment prohibitive (Isaak and Hubert 1997). More importantly, recent work on stream fish movement has challenged the restricted movement paradigm (RMP) that dominated stream ecology theory (Gowan et al. 1994; Schlosser 1995; Gowan and Fausch 1996). This rethinking of the movement of stream fishes suggests that it is important to get a better understanding of the scale of movement of fish at various life history stages and relate this to the habitat structure of a stream.

The consequences of the differing assumptions for fish mobility to the appropriate spatial scale become evident in a comparison of the RMP to the variable movement model (VMM) proposed by Gowan et al. (1994). Integrating these models suggests a gradient of dispersal patterns for salmonids. In all practical and theoretical examples, the location of redds serves as a geographic starting point for passive and active dispersal (Fig. 1). The RMP suggested that salmonids have relatively restricted movements from redds and isolation of family groups would be great (Fig. 1, Gerking 1959; Bachman 1984). Furthermore, the RMP classified moving fish as strays, transients, or nomads that were thought to contribute little to overall production (Gerking 1959; Chapman 1962; Jenkins 1969). For the RMP, the distribution of spawners would be a primary determinant of a river system's production potential within the habitat constraints of natural production units.

New research and re-analysis suggests that the RMP may not always apply and probably does not apply to large juvenile or adult salmonids (Gowan et al. 1994; Fausch and Young 1995). An extreme of the VMM is unlimited

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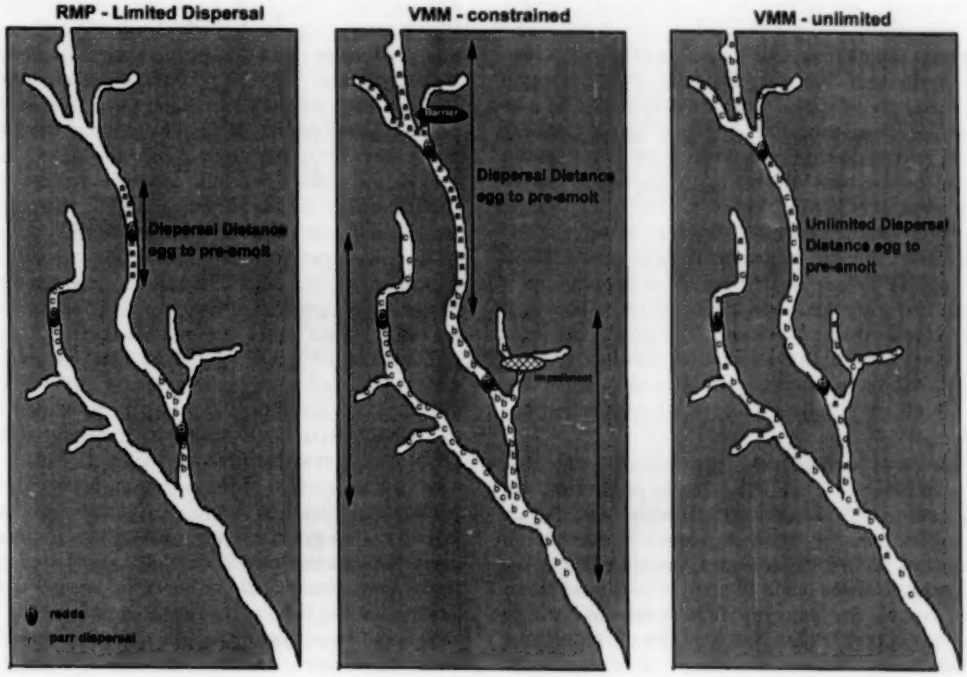
Fig. 1. Three conceptual models of movement and dispersal of juvenile salmonids in streams and their consequences to spatial distribution and population dynamics. Within each panel the capital letter within an oval represents a redd and the lower case letters indicate dispersed juveniles. The left panel represents the RMP advanced by Gerking (1959). Two scenarios for the VMM of Gowan et al. (1994), constrained and unlimited movement are represented in the center and right panels, respectively.



dispersal throughout a watershed (Fig. 1). Intermediate between the extremes of the RMP and unlimited model is a constrained VMM. In a constrained model, dispersal is limited by fish ecology and habitat characteristics. Typically for salmonids, the ability to move increases with size, resulting in a positive relationship between size/age and spatial scale (Gowan et al. 1994; Reeves et al. 1995). However, the ability to move may not be expressed to similar degrees under differential spatial distributions of habitat. In streams that have abundant and highly interspersed habitat for each life stage and season, movement is likely limited because fish do not need to move great distances to acquire requisite resources (Fausch and Young 1995; Schlosser 1995; Gowan and Fausch 1996; Behnke 1997). In streams where habitats are limited and (or) interspersion of necessary habitat types is low, movement is likely to be greater (Fausch and Young 1995; Schlosser 1995; Behnke 1997). Movement also has important genetic and behavioral elements in anadromous salmonids where a size threshold cues emigration from the river system. Another spatial element that influences movement is the location of habitat filters such as barriers or impediments that either totally limit or partially restrict movement. These filters could be natural (beaver dams, falls, stream order, longitudinal gradients, competing species, etc.) or anthropogenic (dams, diversions, changes in thermal regimes, dewatering, introduced species, etc.) and delineation of barriers could be abrupt (dam) or gradual (stream continuum). An additional point that determines the influence of each of these filters is that they may differentially influence movement of juvenile and adult life stages. As a result, in the constrained VMM, the distribution of spawners and the associated movements of juveniles would be joint determinants of a river system's production potential within the habitat constraints of natural production units.

Through our synthesis of elements of spatial habitat structure and fish movement, we conclude that some variant of the constrained VMM is appropriate for most salmonid species, including Atlantic salmon at all life history stages. Furthermore, it seems that defining natural production units for life stages of interest would enhance our understanding of juvenile salmonid production because the structure and spatial distribution of these units would have important population dynamic ramifications. As fisheries scientists develop more sophisticated tools for habitat assessment and gain a better understanding of movement relative to habitat geography, delineating these units will become increasingly feasible. In the next section, we use Atlantic salmon as an example of how natural habitat units may be delineated to focus study on a spatial scale that is consistent with natural production units and may help better understand the interactions between population dynamics and habitat.

Defining riverine production scale for Atlantic salmon parr

We hypothesize that basinwide estimates of salmonid abundance or assessment of habitat modifications on fish production could be improved by partitioning a river into

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natural production units that we call functional habitat units (FHU). FHU are natural partitions (strata) within river systems that contain the necessary habitat elements to support all life history stages through the life stage of interest. The boundaries of a FHU are defined by the spatial arrangement of discrete (spawning, fry, parr, seasonal, etc.) habitat elements, dispersal capabilities, and by filters (barriers or impediments) to dispersal. We view FHU for Atlantic salmon as a nested hierarchy of spatial scale that expands with progressive age/size from submetre (eggs) to global (adults). The FHU for parr production would likely be at a spatial scale between mesohabitat and subbasin for most systems (Williamson et al. 1993; Maxwell et al. 1995) and would contain all of the habitat elements necessary to support Atlantic salmon from the egg to pre-smolt stage. Another key element of the FHU is that the redd serves as the origin of a FHU and that the geographic placement of redds acts as a tether that constrains dispersal options. The goal of delineating these FHU (strata) is that similarities between production capacity, habitat elements, and spawning areas are maximized within FHU and differences are maximized between FHU.

To illustrate how interspersion, juxtaposition, and dispersal influence FHU structure and juvenile production, we present graphical models based on work with a GIS developed from habitat data for the Narraguagus River, Maine, U.S.A. (Beland et al. 1995; Kocik et al. unpublished data). In the Narraguagus River, much of the juvenile production habitat is not suitable for spawning as the substrate is either too large or embedded (Beland et al. 1982, 1995). Thus, spawning habitat is inclusive of rearing habitat but additional rearing habitat exists that cannot be used for spawning and is dependent solely upon parr dispersal. Upon examining habitat data for this river, we observed that the distribution of spawning and rearing habitat varies along the river's length. In the upstream section, spawning and rearing habitat are highly interspersed. In the downriver section, interspersion is lower and some of the rearing habitat is beyond the dispersal distances from larger spawning areas. To examine the role of dispersal upon FHU structure, we bounded Atlantic salmon movement from egg to pre-smolt using values from the literature (Heggenes and Borgstrom 1991; Beall et al. 1994). These studies suggest maximum Atlantic salmon dispersal of 0.4 km upstream and 1 km downstream with densities highest within 0.1 km upstream and 0.4 km downstream from the redd area, decreasing with distance from spawning areas. In addition, the presence of a lake in the middle of the river system forms a seasonal barrier to parr dispersal.

A visual model of FHU delineation can be illustrated by examining a simple stream reach (Fig. 2). In this example, two areas with the same ratio of spawner to juvenile habitat (1:6) and total juvenile habitat (5000 m^2) likely have very different juvenile recruitment dynamics. In the first example, interspersion and juxtaposition are favorable with two spawning areas separated by 1.5 km (Fig. 2A). In this example, a total of 1440 m^2 of river habitat would not be subject to parr dispersal given full utilization of spawning habitat and maximum dispersal distances. This illustrates a natural delineation between upstream and downstream production areas with no overlap in juvenile production. Hence, there are two FHU with juvenile production areas of 1800 m^2 each for a total of 3600 m^2 of utilized habitat.

With a lower interspersion of the two habitat types, all the spawning habitat is restricted to the upper river (Fig. 2B). In this scenario, only 2200 m^2 of the stream would be utilized by spawners in a single FHU. Over 55% of available juvenile production habitat is beyond the documented dispersal maximum. This example illustrates the importance of interspersion of two habitat types and the consequences of juxtaposition. Most habitat models would treat the habitat quality of these two stream sections as equivalent, but including spatial interactions makes it apparent that the stream reach with favorable spatial attributes has the potential to produce 1.6 times the juveniles as the other reach.

To bring these analytical techniques to a watershed level, it is necessary to use GIS to allow more accurate measurements and accounting of river sinuosity. However, the delineation of these units is conducted in the same manner presented above using the spatial arrangement of spawning and juvenile habitat and the assumed dispersal limits. Once GIS data are developed, they can be presented by graphing the parr dispersal area, scaled to spawning area, along the longitudinal gradient of the river (Fig. 3). Such a graph illustrates the interaction of interspersion, juxtaposition, and dispersal capabilities in bounding juvenile production zones (Fig. 3). This graph not only shows the distinctness of the zones but also the magnitude of spawning area that supports production in each one. For example, zone A is 1.5 km long (from river km 6.7 to river km 8.2) and is 9 m longer than zone B but the spawning area contained in zone B (144 metric units) is 2 times greater than that of zone A (72 metric units). This is apparent in the larger area under the curve. In this example, we identified 10 distinct production zones. To simplify simulations for illustrative purposes in the spatial model below, we combined these zones into downstream (zones A–F) and upstream (zones G–J) FHU of the mainstem river.

A spatial model for FHU

To explore the impact of differing FHU structure on presmolt production within a river, we constructed a simple, four-step simulation model (Fig. 4) using a Microsoft Excel workbook format utilizing risk analysis software (@Risk; Palisade 1996). This simulation approach allowed sampling of model parameters from normal or uniform distributions using Latin Hypercube sampling and variable recalculation using Monte Carlo sampling (Palisade 1996). The model is purposefully uncomplicated in order to limit the assumptions needed and focus on the impact of assumptions regarding the spatial arrangement of habitat and spawners.

To start the model, we use the number of female spawners observed in the Narraguagus River system in the autumn of 1996 as the initial condition for generation 0 (K.F. Beland, Maine Atlantic Salmon Authority, Bangor, ME, U.S.A., personal communication). Step 1 of the model determines potential egg deposition by multiplying the number of females by a fecundity variable selected from a normal distribution of the effective fecundity (mean 7560 and SE 1000) for Narraguagus River Atlantic salmon (Baum and Meister 1971).

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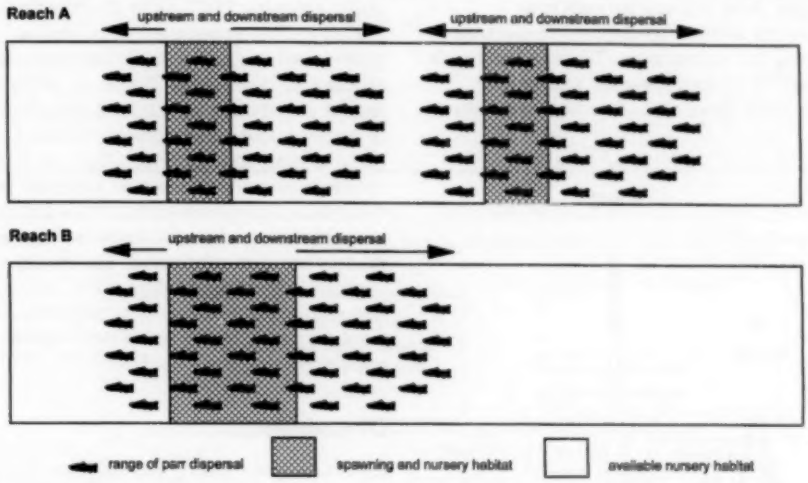
Fig. 2. A graphical representation of the effects of the interspersion and juxtaposition of spawning and nursery habitats upon juvenile production potential in two hypothetical stream reaches with 5000 m^2 of parr habitat and 800 m^2 of spawning habitat. In Reach A, spawning habitat is in two separate regions and dispersal results in two FHU with a net production area of 3600 m^2. In reach B, all spawning habitat is in one reach and dispersal ranges result in single FHU with a net production area of only 2200 m^2.



We calculate parr production from potential egg deposition using a modified version of a linear regression model for a neighboring river (Beland 1996). Because of recent low escapement levels in Maine, no data are available to describe the asymptote of this relationship. To compensate, we capped parr production at 7 parr per metric unit, a level chosen based on maximum densities observed in discrete reaches of Maine salmon rivers since 1950 (K.F. Beland, Maine Atlantic Salmon Authority, Bangor, ME, U.S.A., personal communication). Thus, the resulting algorithm at step 2 becomes a linear regression model with associated standard error (parr = 0.0213 eggs + 1605.04, ±2492 SE) that is truncated by a lower bound of 0 and an upper bound that is determined by the amount of available habitat (Fig. 4). This approach follows the recommendation that a recruitment relationship is a proxy for total habitat quality (Hayes et al. 1996).

At step 3, we calculate the number of outmigrating smolts by multiplying parr production by an overwinter survival estimate selected from a uniform distribution (25 to 60%) based on other studies in New England (Orciari et al. 1994; Whalen et al. 1996). At step 4, we calculate total adult returns by multiplying total smolt production by a marine survival variable selected from a uniform distribution (0.75% to 5%) based on the range of values in the literature and recent simulation studies on the Narraguagus River (Bley and Moring 1988; Anonymous 1996; Friedland 1998). The final output for the initial generation becomes the input for the next generation and continued for 50 successive generations. Additional assumptions of this model are a 1:1 sex ratio and no cross-over of age classes (smolt at age-2 and return as 2 sea-winter adults). We chose this approach because deviations from this life history pattern are minimal and tests with more complicated overlapping age-classes yielded similar results.

Each iteration of the simulation was run until the population was extirpated or reached 50 generations. Three summary variables provide useful indices of the results: extirpation probability, average parr production, and generations to recover. The extirpation probability is the likelihood that the population will fall below two spawners within 50 generations. When the population survived, a useful index value was the average parr production over 50 generations. This value represents the juvenile production capacity and is presented with its standard deviation and coefficient of variation. Our final index value was generations to recover; this value was the number of generations for parr production to reach the mean parr production level for that iteration. All simulations were run until these three output variables converged at variance levels of less than the 1.5% level; for most simulations this was between 1800 and 2000 iterations.

To explore the impact of ignoring the importance of habitat interspersion and juxtaposition in delineating FHU, we ran a baseline simulation that treated the Narraguagus River as a single FHU (Fig. 4) comprised of 6017 metric units (1 metric unit = 100 m^2) of parr habitat. This baseline simulation for the Narraguagus River parr habitat yielded an extirpation probability of 17.8% and production averaged 15 552 (±4 456) Atlantic salmon parr (Table 1). Because our study river exhibits few filters to adult dispersal but contains spatial filters to juvenile dispersal, we felt it was important to examine a scenario of unlimited adult access with habitat constrained juvenile dispersal. As such, we partitioned the 6017 metric units of parr habitat into three distinct FHU based on previous habitat research in the Narraguagus River (Beland et al. 1995; Fig. 5; Table 1). The majority of juvenile production habitat is located in the mainstem with 3544 metric units in the lower mainstem FHU and 1989 metric units in the upper mainstem FHU. The west branch FHU constitutes 484 metric units, or 8%, of the basinwide total.

Because no definitive model for within-river dispersal of spawners is available, we explored the implications of four spawner distribution scenarios (homing, preference, propor-

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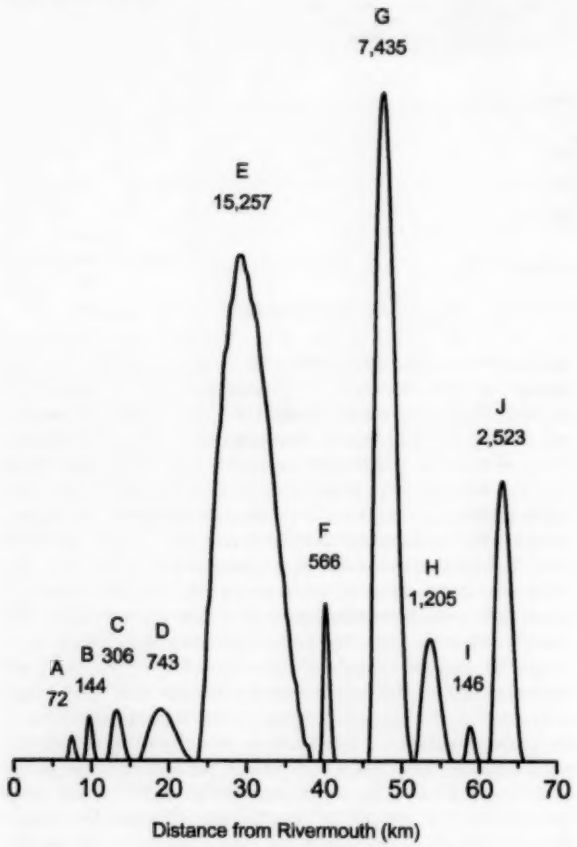
Fig. 3. A generalized graphical representation of juvenile distribution zones and associated spawning areas in Narraguagus River mainstem reaches based on original data from Beland et al. (1995). The X-axis represents the distance upstream from the head of tide; the distance along this axis for each zone represents the upstream and downstream dispersal of juveniles from connected spawning and rearing areas. The area under each hyperbola is proportional to the total spawning area in that production zone and is listed above each curve in metric units (1 unit = 100 m^2).



tional, and semi-random). The homing scenario assumed that the number of females returning to each FHU varied based on previous parr production in each FHU. The preference scenario assumed that spawners have a general preference for individual FHU based on distance from the ocean and FHU spawner density. We simulated this scenario using a three-tiered function with a density dependent sequential preference for the lower mainstem, upper mainstem, and west branch FHU. The proportional scenario allocated females using constant proportions based on total spawning habitat in each reach. The semi-random scenario allocated spawners first based on a 0–8% probability of spawning in the west branch FHU and then by a 0 to 92–100% probability of spawning in the lower mainstem or upper mainstem FHU. For initial model inputs we used the actual geographic distribution of female spawners, represented by redd counts observed in the Narraguagus River system in the autumn of 1996 (K.F. Beland, Maine Atlantic Salmon Authority, Bangor, ME, U.S.A., personal communication).

Results from this group of simulations indicate that artificially grouping FHU, as in the baseline scenario, would potentially overestimate extirpation probability and generations-to-recover while underestimating long-term parr production capabilities (Table 1). Different scenarios of the spatial distribution of adults highlights the potential effects of varying these assumptions (Table 1). The magnitude of these assumptions is compelling as it suggests a 48% increase in juvenile production potential and near 60-fold difference in extirpation probabilities between the baseline and proportional models. Differences between the intermediate models are also substantial. The results of these simulations suggest that understanding FHU structure and the factors that regulate site-selection by spawners will allow for significant increases in the precision of production estimates and population dynamics analyses.

Discussion

As theory regarding the mobility of juvenile salmonids in streams has evolved (Gowan et al. 1994; Gowan and Fausch 1996), the importance of determining the appropriate scale for assessing parr production and population dynamics emerges as critical for accurate determination of basin-scale production dynamics. Our simulations of Atlantic salmon parr production in the Narraguagus River show that segmentation of a basin into distinct FHU, relevant to the juvenile stage, lends stability to population structure within a riverine stock and leads to less variation in estimates of total parr production in the basin. We believe that this is particularly true of anadromous salmonids because adults can pass habitat filters that juveniles may not be able to pass physically or behaviorally, thus bounding FHU for juvenile production. These conclusions are analogous to those for metapopulations that examine the demographic stability between populations or stocks (e.g., Schlosser 1995; Schlosser and Angermeier 1995). However, the stability that is exhibited by increased FHU complexity is driven by habitat-based spatial segregation within a stock across a spatially complex habitat. The two key assumptions of this stratification are that isolated segments of juvenile rearing habitat exist and that biotic potential (eggs) is determined by spawning site selection that is more complex than simple homing.

Some fragmentation or isolation of distinct habitat areas for juvenile production is likely common in most watersheds large enough to sustain a stock in relative isolation leading to multiple FHU within a river system. While at the extreme the genetic isolation of these units would establish stocks, restricted juvenile dispersal within a stock at the FHU level would provide buffers to environmental extremes at the basinwide level. The reasons for increased stability and production potential are two-fold. First, even at low spawner densities, if all fish spawned in one area, density-dependent factors would lead to decreased production as compared to a population with dispersed spawners. Second, the filters and other parameters that delineate FHU structure often result in units that react differently to extreme environmental conditions. For example, an upstream FHU may be more suitable

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Table 1. Index values of simulation models of Atlantic salmon populations for extirpation probability, generations to recover, average parr production (years 1–50) with its associated standard deviation and coefficient of variation (C.V.).

Model name	Extirpation probability (%)	Generations to recover	Parr production	Standard deviation	C.V. (%)
Single FHU – baseline	17.8	18.7	15 552	4456	28.65
3 FHU – homing	7.4	14.8	18 570	4649	25.04
3 FHU – semi-random	2.6	15.2	18 827	2285	12.14
3 FHU – preference	1.4	15.4	20 363	2343	11.51
3 FHU – proportional	0.3	7.8	23 096	2096	9.08

Fig. 4. Flow chart and schematic of a basic simulation model of juvenile Atlantic salmon production on a watershed scale. The model is initiated with the number of female spawners present in year 0. Resultant output from one generation of the model are the starting values for the next generation.

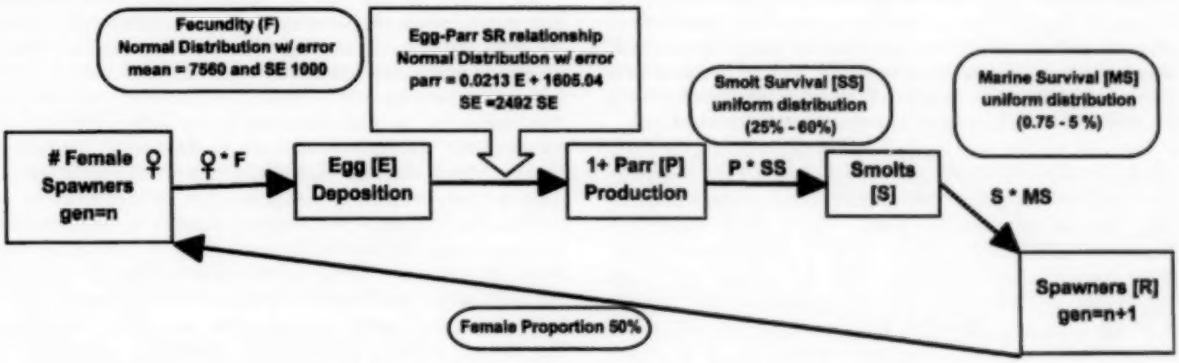
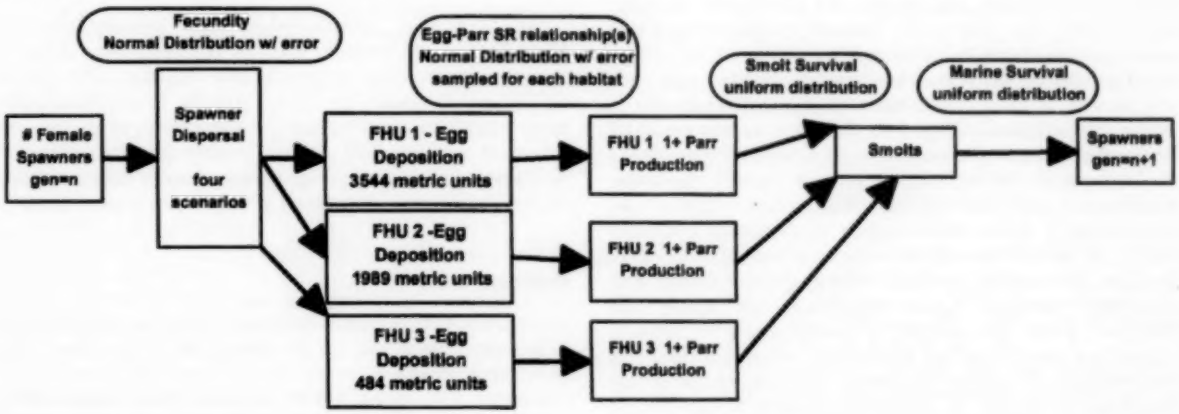


Fig. 5. Flow chart of a simulation model of juvenile Atlantic salmon production with variable spawner dispersal between three distinct FHU of juvenile production within a watershed.



during a warm wet summer while a downstream FHU is more suitable during a dry cool summer. As such, these habitat units would respond differently to different environmental conditions. These differential responses act to dampen the overall effects of environmental extremes within a basin. Our simulation results underscore these points, suggesting that, for Atlantic salmon, the presence of multiple FHU within a river basin is beneficial to persistence at low population levels and leads to increased juvenile production. As a result, a more complex FHU structure would serve to make a population more productive and stable over time. However, excessive fragmentation is also of concern since the amount of critical habitat can become too isolated from other habitats to maintain adequate linkage (spawner dispersal) between the habitat units.

In the Narraguagus River example, FHU delineations are primarily a consequence of natural geological structure. In other systems, these delineations may be driven primarily by anthropogenic effects — the presence of impoundments, alteration of channel structure, instream flow issues, etc. A

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frequent conclusion of studies of the spatial elements of fish habitat is that habitat fragmentation is a major problem (Schlosser 1991; Lohr and Fausch 1997; Schlosser and Angermeier 1995). Loss of connectivity and complete isolation of stream reaches are obvious and chronic detriments to the natural structure of stream fish communities. Using the FHU approach, the challenge to fishery managers in perturbed systems would be to determine the extent to which anthropogenic factors have either fragmented the habitat (separated FHU that were previously contiguous) or simplified habitat (decreased FHU number and inter-FHU differences) from baseline conditions. Clearly, as the quality of the habitat degrades in even one FHU, total juvenile production in the river decreases. This is an important consideration because decreased production could be the result of reduced habitat quality in only part of a watershed (i.e., only in one FHU). If habitat is degraded in a preferred spawning reach, these changes will be further accentuated. As such, using a FHU approach could identify a geographic area of greatest production significance, focusing habitat rehabilitation efforts or protection efforts where they are needed the most.

Our simulations also suggest that changes in overall smolt production are caused not only by changes in FHU complexity within the basin but also by changes in spawner distribution patterns between the FHU. The optimal theoretical model of distribution appears to be a proportional model since the extinction probability and generations to recover are lowest and long-term parr production are the highest with low variation. However, this model may be difficult to defend biologically as it requires a population of spawners to distribute itself optimally in relation to available habitat within the basin (Bartholow et al. 1993; Williamson et al. 1993). Thus, a combination of the preference and semi-random models may best explain the distribution of redds among FHU. We believe that there is strong evidence that spawning site choice by salmonid populations within rivers is influenced by discharge, temperature, and spawner density, as well as natal stream reach (Kocik and Taylor 1987). Given this hypothesis, if spawner distributions between FHU (defined at the juvenile scale) can be quantified and related to demographic, behavioral, or environmental factors, the variance of stock-recruitment relationships may be decreased and a better understanding of basinwide dynamics will occur. In addition, this has important management ramifications for establishing target spawning requirements that frequently disregard spatial distribution (O'Connell and Dempson 1995). For example, spawning targets for Atlantic salmon are often based on desired egg deposition rates and the fecundity of females. If spawner levels in excess of this threshold are needed to distribute spawners throughout all reaches of the watershed, the target levels may be insufficient.

Through our synthesis of recent developments in spatial analysis of fish habitat, salmonid ecology, and salmonid movement in streams, we conclude that Atlantic salmon populations likely function in a manner that supports the hypothesis that the spatial arrangements of habitat components can give rise to markedly different population dynamics at various spatial scales (Grossman et al. 1995; Schlosser 1995). An interesting component of this hypothesis is that it highlights the need to integrate physical habitat data with traditional population dynamics (mortality, fecundity, immigration, and emigration). Additionally, a spatial approach should become a mechanism to broaden habitat models and move away from the general assumption that fish populations are solely limited by physical habitat to a more holistic approach that integrates biotic factors such as competition, predation, and fisheries (Fausch et al. 1988; Hayes et al. 1996).

We believe that the FHU approach provides a framework that uses the spatial distributions of habitat in concert with data on stage-specific habitat utilization, dispersal, and habitat filters to define natural units at various scales. The advent of more precise and user-friendly methods for measuring, interpreting, and modeling habitat (i.e., global positioning systems and GIS; Isaak and Hubert 1997) provide new opportunities for analysis at various spatial scales. These new methods will enable researchers to quantitatively examine differences in salmonid production to assess the impact of interspersion and juxtaposition of discrete habitat units within and between FHU. While the case-study explored in this manuscript highlighted primarily the abiotic elements of habitat, FHU structure should also be defined by the occurrence of biotic factors that would restrict fish distribution ranging from diseases to competing fish species to avian or mammalian predators. The baseline habitat, movement, and ecological data needed to delineate FHU is substantial, but when these data are available, determining appropriate scale for a life stage will improve resolution of analyses of population dynamics, habitat management, and other evaluations that assume a closed population or population segment.

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Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams

N. LeRoy Poff and Alexander D. Huryn

Abstract: Understanding variation in the freshwater production of Atlantic salmon across its range is a critical aspect of the species' conservation, restoration, and management. We focus on how environmental factors operate at four hierarchical scales (region, watershed, reach, local habitat) to influence the production and survivorship of juvenile salmon and the production of their invertebrate food base. Using published, quantitative information about invertebrate production in small, cold streams characteristic of Altantic salmon nursery streams, we estimate expected maximum salmon production will be ca. 9 (range 6–22) g wet mass · m^{-2} · $year^{-1}$, which compares favorably with reported literature values of <1 to 17 g · m^{-2}. We highlight some empirically based, shortcut approaches to estimating invertebrate production that may be particularly useful for evaluating salmonid production across a range of scales. We also consider how availability of invertebrate prey may influence salmon production. As a synthesis, we integrate existing information into a multi-scale framework by making qualitative predictions (hypotheses) about expected patterns of invertebrate and salmon production at different habitat scales. We then develop quantitative, heuristic scenarios that predict (hypothesize) how salmon and invertebrate production will change in response to selected physicochemical and non-trophic habitat limitations operating at the watershed (geology, land use) and reach (channel form, canopy) scales. Predicted values, which fall within the range of observed values for Atlantic salmon streams, demonstrate that a multi-scale habitat perspective can provide important insights into local to regional variation in the production of Atlantic salmon across its range and thus contribute to Atlantic salmon conservation, restoration, and management.

Résumé : Il est primordial de comprendre la variation dans la production dulcicole du saumon atlantique dans son aire de répartition pour assurer la conservation, le rétablissement et la gestion de cette espèce. Nous mettons l'accent sur la manière dont les facteurs environnementaux agissent à quatre échelles hiérarchiques (région, bassin, tronçon de cours d'eau et habitat) pour influer sur la production et la survie des saumons juvéniles, de même que sur la production des invertébrés dont ils se nourrissent. À l'aide de données quantitatives publiées sur la production d'invertébrés dans les petits cours d'eau froids qui constituent typiquement les alevinières du saumon atlantique, nous estimons la production de saumon maximale attendue à environ 9 (fourchette de 6 à 22) g de poids frais par m^2 et par année, ce qui se compare favorablement aux valeurs signalées dans la documentation scientifique (<1–17 g · m^{-2}). Nous présentons des méthodes empiriques abrégées d'estimation de la production d'invertébrés qui peuvent être particulièrement utiles pour évaluer la production de salmonidés à diverses échelles. Nous examinons aussi comment la disponibilité des invertébrés proies peut influer sur la production de saumons. À titre de synthèse, nous constituons avec les données existantes un cadre multi-échelles en faisant des prévisions qualitatives (hypothèses) concernant les profils attendus de production d'invertébrés et de saumons à différentes échelles d'habitat. Nous établissons par la suite des scénarios heuristiques quantitatifs qui prévoient (de manière hypothétique) comment la production d'invertébrés et de saumons changera en fonction de facteurs physicochimiques et non trophiques limitants liés à l'habitat et agissant aux échelles des bassins (géologie, utilisation des terres) et des tronçons de cours d'eau (forme du chenal, couvert végétal). Les valeurs prévues, qui tombent dans la fourchette des valeurs observées pour les cours d'eau à saumon atlantique, montrent qu'une approche prenant en compte l'habitat à diverses échelles peut fournir des perspectives intéressantes sur la variation aux échelles locale à régionale de la production du saumon atlantique dans l'ensemble de son aire de répartition, et ainsi contribuer à la conservation, au rétablissement et à la gestion de l'espèce.

[Traduit par la Rédaction]

Introduction

The freshwater phase of the Atlantic salmon (*Salmo salar*) life cycle is a critical period in which reproduction, early growth, and survivorship set limits to production. Between spawning and smolt outmigration, production of young salmon depends on at least three broad environmental factors: an adequate food supply, suitable physical habitat, and

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N.L. Poff. Department of Biology, Colorado State University, Fort Collins, CO 80523-1858, U.S.A.
A.D. Huryn. Department of Biological Sciences, 5722 Deering Hall, University of Maine, Orono, ME 04469-5722, U.S.A.

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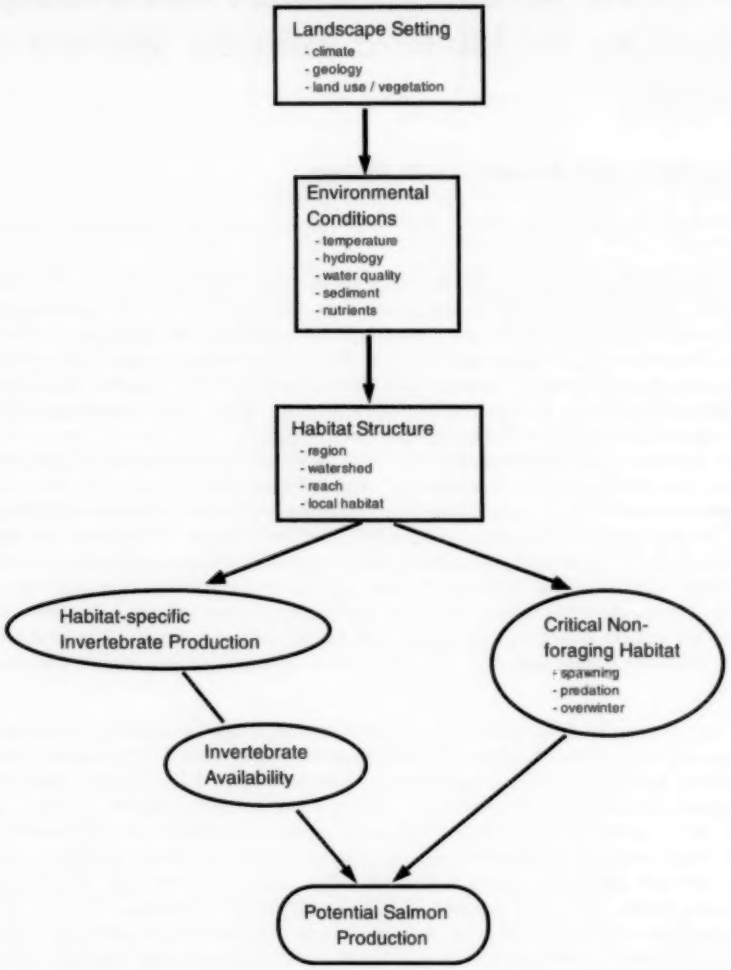
Fig. 1. Conceptual overview of multi-scale, landscape framework for secondary production.



favorable physicochemical conditions. Juvenile salmon production can be limited by any one of these factors, a fact long appreciated (e.g., Lindroth 1965; Chapman 1966*a*). However, their relative importance is poorly understood, as is the extent to which they may interact to limit salmon production or change geographically in response to landscape and climatic features. A better understanding of these factors and their interactions is needed to facilitate the conservation, restoration, and management of Atlantic salmon.

Production is an integrated response to constraints and opportunities posed by abiotic and biotic processes and conditions that occur at a variety of spatial and temporal scales. Accordingly, production provides a comprehensive measure of ecological performance. Identifying spatial and temporal scales at which factors limiting production are most effectively expressed should improve our understanding of landscape variation in Atlantic salmon production. The hierarchical conception of stream habitat (e.g., Frissell et al. 1986) is most suitable for this task because it provides a multi-scale framework for assessing factors operating at different scales, ranging from local habitat to whole watersheds to geographic regions. By calling attention to multiple constraints and processes, a multi-scale framework provides a general and realistic approach for the examination of ecological patterns (e.g., Imhof et al. 1996; Rabeni and Sowa 1996; Richards et al. 1996; Poff 1997). A better understanding of multi-scale constraints on Atlantic salmon production will allow us to better define the productive capacity of present populations and better identify areas where conditions could support viable salmon populations in the future.

In this paper, we consider how environmental conditions, habitat features, and invertebrate production limit salmon production in a multi-scale context (Fig. 1). Habitat and environmental conditions may directly limit salmon production by influencing survivorship, or they may indirectly limit salmon production by influencing prey production and availability. Because invertebrate production represents the transformation of a stream's energy base to a form available to juvenile salmon, consideration of different pathways providing support for invertebrate production in salmon nursery streams is necessary before fundamental factors that may limit salmon production can be identified. Although obvi-

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ously not the only factor limiting salmon production, we pay particular attention to invertebrate prey production, because knowledge of this factor will allow guesses about maximum potential production of juvenile salmon (Richardson 1993). Despite the importance of prey production in determining salmon production, knowledge about this critical aspect of salmonid ecology in general, and Atlantic salmon ecology in particular, is surprisingly obscure (Waters 1993; Richardson 1993; Huryn 1996).

Secondary production

In its broadest sense, "secondary production" refers to the formation of heterotrophic biomass over time (Benke 1993). Annual secondary production for a population of juvenile Atlantic salmon inhabiting a specific nursery stream, for example, will be the sum of all biomass produced by that population during a 1-year period (e.g., $g \cdot m^{-2} \cdot year^{-1}$). This summed production will include the new biomass actually remaining at the end of the year and all losses that occurred during that year. Losses may include mortality (disease, cannibalism, predation), loss of tissue reserves (starvation and mucous production), and emigration. Secondary production thus clearly differs from other measures commonly used to indicate the productivity of salmon nursery streams. "Smolt production," for example, refers to the number of smolt that leave a given nursery stream (e.g., smolt $area^{-1} \cdot time^{-1}$; Meister 1962; Mills 1989; Power and Power 1992). Although of obvious importance for management concerns, indicators such as smolt production do not necessarily provide information about the actual energy base of a given stream or how this energy is apportioned among different functional and trophic pathways.

Measurement of secondary production, at minimum, requires information about growth rate and biomass for the target population. Growth rate can be measured either directly from marked or confined individuals (invertebrates, fish), or as a function of size-at-age as indicated directly by growth rings deposited in bony structures (fish) or indirectly by population size structure (invertebrates, fish). The numerous methods for directly estimating secondary production are summarized in the excellent reviews by Bagenal (1978) and Benke (1984; 1993). Obtaining estimates of production for fish populations in small streams is relatively easy. For their invertebrate prey, however, such is not the case, due both to the large number of samples required for reasonably precise estimates of biomass in systems that are notoriously variable in space and time, and to difficulties in removing cryptic invertebrates from samples. Further, estimates of invertebrate secondary production for *entire stream communities* must be composites of measurements conducted separately for numerous species of consumers that may differ markedly in life histories and habitat distribution. Because of these difficulties, there are relatively few whole system estimates of macroinvertebrate production in streams and rivers (~40 streams; Benke 1993), even fewer for salmonid streams (~12 streams; Waters 1988; Huryn 1996). To our knowledge, there are no estimates for streams that currently support populations of Atlantic salmon; however, estimates do exist for two tributaries of the Connecticut River (Massachusetts) that probably contained populations of Atlantic salmon early in the nineteenth century (Fisher 1977; Neves 1979).

Given the high labor costs required to directly measure invertebrate production, shortcut approaches are needed. Of the several offered (Benke 1984; 1993), two seem to hold reasonable promise. The first is based on the annual biomass turnover rate (annual production/mean annual biomass), or "P/B," which is a rough estimator of the average annual instantaneous growth rate for the target population. Waters (1969) showed that the P/B for cohorts within populations of invertebrates fell within a relatively narrow range (2–8), and suggested that *cohort production* might be estimated as the product of biomass and a suitable P/B (5 is usually suggested). When entire benthic communities are considered, however, the range of P/Bs for *annual production* varies from <1 to 117 because cohorts of different taxa may require periods of several weeks to several years (Benke 1993). The range of expected annual P/Bs can be narrowed by considering only small temperate streams (e.g., mean discharge ~0.1 to 1.0 $m^3 \cdot s^{-1}$ and mean annual temperature 5–10°C), where annual P/Bs range from 2.2 to 8.7 (10 streams) or from 4.2 to 7.9 (7 streams) (Benke 1993). The P/B approach for estimating production also has applications for fish as well as invertebrates. The P/B for populations of brown trout (*S. trutta*), for example, can be accurately estimated as a function of age structure (Waters 1992; see also Kwak and Waters 1997).

The second genre of promising shortcut approaches is the development of multiple regression models that estimate invertebrate production as a function of more readily measured variables, usually temperature, population biomass, and maximum body size (Morin and Bourassa 1992; Benke 1993; Morin and Dumont 1994; Benke et al. 1997). Similar equations are available for stream fish populations (e.g., Randall et al. 1995). The potential for estimating annual production of juvenile Atlantic salmon as a function of standing stock biomass, either mean annual or measured at a specific time of the year, is apparent from plots provided by Gee et al. (1978) and Randall and Paim (1982). The empirical approach has been criticized because it is prone to imprecision and inaccuracy, particularly when used to estimate production for single species at a single location (Benke 1993). However, the estimation of production for entire communities or groups of species (e.g., functional groups) as summed composites of estimates for single populations may increase the accuracy of this method (Benke et al. 1997). Indeed, using a variation of the regression approach, Benke (1993) and Webster et al. (1995) showed that production of invertebrate functional feeding groups (sensu Cummins 1973) may be estimated as various linear and polynomial functions of stream size (as indicated by mean annual discharge). These equations are particularly compelling because they may allow invertebrate production to be partitioned into categories of prey that differ in availability and quality (e.g., assimilability) for salmonids (cf. Wootton et al. 1996; Rader 1997), show different levels of dependence of secondary production on riparian and watershed energy and nutrient sources (Doucett et al. 1996), and follow patterns that may change with stream size in predictable ways (Vannote et al. 1980). The testing and refinement of the application of such empirical approaches for estimating secondary production merits fur-

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ther research because they may be particularly useful for estimating biologically reasonable ranges of production at large spatial scales required for multi-scale studies of stream ecosystem processes (e.g., among general categories of streams).

Evidence for food-limitation of salmonid production

Published research on stream salmonids suggests that limitation of Atlantic salmon production by invertebrate production cannot be easily dismissed, especially in nutrient-poor waters (see Richardson 1993). Several studies have shown positive correlations between food abundance in streams and salmonid growth rates (Wilzbach et al. 1986; Erkinaro and Niemela 1995), biomass (Murphy et al. 1981; Bowlby and Roff 1986*b*) and abundance (Slaney and Northcote 1974). Experimental support for food-limitation of fish in salmonid streams also exists. In an early study, Mason (1976) amended food supply to juvenile coho salmon (*Oncorhynchus kisutch*) in British Columbia headwater streams and observed an increase in growth rates and lipid storage. Peterson et al. (1993) used stable isotope analysis to show that the addition of inorganic fertilizer to an oligotrophic Alaskan river resulted in rapid increases in benthic algal and insect production; within 3 years, increased growth rates of young-of-year and adult grayling (*Thymallus arcticus*) were attributed directly to enhanced algal production. Similarly, in a forested British Columbia stream, nutrient addition stimulated primary productivity and increased the weights of two species of salmonid fry (Johnston et al. 1990).

In Atlantic salmon streams, however, there is mixed evidence for food limitation. Studies showing a positive relationship between prey abundance and salmon biomass (e.g., Egglishaw 1967; Gibson and Galbraith 1975; Gibson and Dickson 1984), and density-dependent growth cohorts of Atlantic salmon in Norway (Bergheim and Hesthagen 1990; Heggenes and Borgstrom 1991) suggest that food limitation can occur. In addition, Erkinaro and Niemela (1995) showed that high growth rates of Atlantic salmon among tributaries of a Finland stream system were related with high levels of drifting prey. By contrast, however, a 10-year study of juvenile Atlantic salmon production in the Miramichi and Restigouche rivers (New Brunswick) showed that annual variation in growth rate was minimal and independent of fish abundance (Randall and Chadwick 1986). Production was most closely related to population abundance and biomass rather than growth rate. Since food limitation was clearly not a factor in determining production, Randall and Chadwick (1986) suggested that non-trophic factors that influenced recruitment — overfishing of adult salmon was specified — controlled abundance and maintained juvenile salmon production below carrying capacity. Gee et al. (1978) similarly reported that production of Atlantic salmon in the River Wye (Wales) was controlled by spawning success rather than prey availability.

Guesses about trophic support for juvenile Atlantic salmon

Waters (1988) reviewed studies of salmonid – invertebrate production relationships worldwide to show that maximum levels of annual production by populations of stream dwelling salmonids (primarily brown trout) ranged to 36 g wet mass (WM) $\cdot$ m^{-2}, with levels >10 g WM $\cdot$ m^{-2} indicating "productive" streams. Similar data for populations of juvenile Atlantic salmon, however, are scarce. Randall and Chadwick (1986) summarized production data for seven streams around the North Atlantic to show that mean annual production ranges from <1 to about 9 g WM $\cdot$ m^{-2}. The maximum levels of annual production yet reported are 16–17 g WM $\cdot$ m^{-2} (Mann 1971; Bergheim and Hesthagen 1990). It is clear that production by juvenile Atlantic salmon can attain levels expected for productive trout streams.

Wet mass can be converted to ash-free dry mass (AFDM), which is more easily used for comparisons, using conversion factors provided by Waters (1988). The mean annual production of 8.9 g WM $\cdot$ m^{-2} reported for Atlantic salmon in the Shelligan Burn (Egglishaw and Shackley 1977), for example, is roughly equivalent to 1.6 g AFDM $\cdot$ m^{-2} $\cdot$ $year^{-1}$. Based on a food conversion efficiency of 0.2 for salmonids (Waters 1988), 1.6 g AFDM of annual salmon production will require roughly 8.0 g AFDM $\cdot$ m^{-2} of annual prey production with 100% utilization.

Egglishaw (1970) reported that the mean standing stock of benthic fauna in the Shelligan Burn measured during a single year (1962–1963) was 2.9 g dry mass (DM) $\cdot$ m^{-2} (roughly equivalent to 2.6 g AFDM $\cdot$ m^{-2}). Egglishaw and Shackley (1985) later reported a standing stock of 1.2 g DM $\cdot$ m^{-2} (~1.1 g AFDM $\cdot$ m^{-2}), a value presumably based on a survey conducted in 1969–1970 (Egglishaw and Shackley 1977). Assuming that the mean of these values estimates the expected standing stock of prey during the study, the turnover rate required to provide prey production that matches the estimated consumption is 4.2 (=8.0/1.9). This turnover rate is clearly realistic, given that turnover rates as high as seven are not unexpected for benthic invertebrate communities in temperate streams similar in size (mean discharge = 0.12 $m^{-3} \cdot s^{-1}$) and mean temperature (~7°C) (Benke 1993).

Atlantic salmon are not the only species of fish in the Shelligan Burn, however. There are also populations of brown trout and eels (Egglishaw and Shackley 1977). The combined mean annual production of brown trout and Atlantic salmon during the study was 19.2 g WM $\cdot$ m^{-2} (~3.5 g AFDM $\cdot$ m^{-2}; eel production was not measured). The turnover rate of benthic invertebrate biomass required to support this combined production is roughly 9.2. This turnover rate is unreasonably high (Benke 1993). The preceding calculations are based on the assumption that both trout and salmon feed exclusively on benthic invertebrates. Egglishaw (1970), however, reports that terrestrial invertebrate prey may comprise ~30% of total prey consumption by brown trout, and ~23% for Atlantic salmon in the Shelligan Burn. Assuming that consumption of terrestrial prey is only 20%, the turnover rate of benthic prey required to meet the demands of both trout and salmon is 7.4. Although in the high range expected for streams similar to the Shelligan Burn, this turnover rate is clearly realistic (cf. Benke 1993), and is similar to the turnover rate of 7.1 to 7.4 reported by Neves (1979) for macroinvertebrates associated with cobble habitat in what was presumably an historical Atlantic salmon stream in New England.

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A probable maximum amount of invertebrate prey production expected for salmon streams can be determined, using a summary table provided by Benke (1993). Streams with a mean annual temperature ≤8.5°C and mean annual discharge ≤1 $m^3 \cdot s^{-1}$, and without significant organic pollution, are expected to have levels of invertebrate production ranging from about 4 to 24 g AFDM $\cdot m^{-2} \cdot year^{-1}$, with values ≤8 g AFDM $\cdot m^{-2} \cdot year^{-1}$ being most common (7 out of 9 reports, Benke 1993). Assuming a 20% energetic efficiency (Waters 1988), and assuming that no prey production is lost to pathways other than salmon predation, the maximum salmon production expected for nursery streams will range from about 0.8 to 4.8 g AFDM $\cdot m^{-2} \cdot year^{-1}$ (=6 to 22 g WM), with levels of about 1.6 g AFDM $\cdot m^{-2} \cdot year^{-1}$ (=8.9 g WM) the most reasonable maximum expected level. These estimates reflect reported literature values of annual salmon production that range from <1 to about 9 g WM $\cdot m^{-2}$, with an extreme maximum of 17 g WM $\cdot m^{-2}$ (Mann 1971; Randall and Chadwick 1986).

On the basis of these admittedly "back of the envelope" calculations and sparse data, it appears that the higher ranges of production reported for Atlantic salmon streams may be accommodated by reasonable levels of benthic prey production. However, it should also be noted that production by predatory invertebrates and other fish will also require some of the benthic prey production which will reduce that available to salmon. Accordingly, since it appears that a significant proportion of prey production may at times be required to support juvenile salmon production, the potential for the coupling of these two compartments can be strong. Terrestrial invertebrates may also provide an important subsidy to the diet of juvenile salmon that will reduce pressure on benthic prey, yet the quantitative significance of terrestrial invertebrates as a source of food for salmon is poorly understood. Finally, it should be noted that over the 10-year period that Atlantic salmon production was measured in the Shelligan Burn, annual production ranged more than twofold (5.5 to 12.1 g WM $\cdot m^{-2}$; Egglishaw and Shackley 1977). Factors underlying such long-term temporal variation must be identified before a predictive knowledge about the interrelationship between production of Atlantic salmon and their prey can be attained.

Is "invertebrate production" equivalent to "prey production" for juvenile Atlantic salmon?

Benthic prey

Juvenile Atlantic salmon are opportunistic foragers, able to switch between benthic and drift feeding depending on relative abundance of preferred prey (e.g., Gibson 1993). Recent experimental work, however, indicates that salmon parr spend a majority of their time feeding directly from the drift, even when drift availability is locally reduced (Nislow et al. 1998). Therefore, it would appear that juvenile salmon acquire much (if not most) of their energy by drift feeding, and factors that reduce the availability of drifting invertebrates to salmon may present a bottleneck to salmonid production.

Benthic invertebrates have different tendencies to drift and are thus differentially available to drift-feeding salmonids (Waters 1972). Compared to species that are common components of drift, those that do not drift frequently will be less available to salmonids, either because they are cryptic (e.g., some cased caddisflies) or because they are inaccessible (e.g., interstitial fauna). Recent work showing competitive suppression of palatable, drifting prey by invulnerable prey (Power et al. 1996; Wootton et al. 1996) indicates that estimates of gross invertebrate production alone may not be sufficient to understand limits on salmon production; consideration of community composition and relative availability of potential prey may also be required. If this is the case, then a functional approach that characterizes the availability of invertebrate guilds to drift-feeding salmonids would be valuable. Ideally, guilds should be defined to satisfy two conditions: (1) differential availability to salmon predators (to translate benthic production to potential salmon production), and (2) differential sensitivity to environmental conditions (to understand landscape variation in conditions that constrain invertebrate guild availability).

The ecological implications of differential availability have recently been examined by Rader (1997), who classified 95 benthic invertebrate taxa in the central Rocky Mountain region (U.S.A.) into availability guilds for drift-feeding salmonids. He used a number of behavioral and microhabitat preference characteristics that are likely to influence drift entry (e.g., mobility, exposure to flow, body size). When ranked according to availability, the taxa showed significant correlations with the actual ranks of invertebrates in trout stomach contents as reported in three published studies. The most available taxa included the mayfly *Baetis*, blackfly (Simuliidae) larvae, and amphipods, all widely distributed and known as "drifters" (e.g., Waters 1972). The most unavailable taxa consisted mostly of species occupying hyporheic or depositional habitats (including burrowing species). Taxa with intermediate availability occurred in erosional areas, but were not generally found in microhabitats fully exposed to flowing water. In general, species that actively swim or drift and reside in flow-exposed microhabitats (e.g., *Baetis* and simuliids) are most available to drift-feeding salmonids. These findings imply that, all other factors being equal, Atlantic salmon production should be greater in streams having high relative production of these drifting invertebrate species.

Terrestrial prey

Terrestrial invertebrates may at times be important sources of food for stream fishes in general (Chapman 1966*b*; Hunt 1975; Waters 1993), and juvenile Atlantic salmon in particular (Egglishaw 1970; Gibson and Cunjak 1986). Terrestrial invertebrates, for example, have been shown to be important prey for juvenile Atlantic salmon in Scotland and Newfoundland (Egglishaw 1970; Gibson and Cunjak 1986), and they are almost certainly important across the Atlantic salmon's entire range. These studies indicated that terrestrial invertebrates may at times compose >20% of the stomach content. Such reports, however, tend to obscure how seasonal patterns of the relative availability of prey in salmon streams may magnify the importance of terrestrial sources of prey to salmon survival. In heavily forested, oligotrophic streams, in particular, the life cycles of many invertebrate species are synchronized with the input of leaf detritus during the autumn. Growth occurs during autumn and spring,

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with adult insects emerging in late spring and early summer. As a result, the biomass of benthic invertebrate prey may be at its lowest point during summer, when metabolism of salmon is maximal due to summer water temperatures (Hynes 1970; Hunt 1975; Cada et al. 1987; Garman and Moring 1993). The summer period may represent an energetic "bottleneck," and the importance of terrestrial invertebrates to the survival of juvenile salmon may be much greater than indicated by quantitative considerations of stomach content alone. Mason (1976) supported this view by showing that growth and survival of coho salmon in British Columbia was food-limited during the summer months, and that salmon size and density were increased several fold by experimental feeding. If a similar relationship occurs in Atlantic salmon streams, riparian inputs of terrestrial invertebrates have clear implications for management of salmon streams for maximum salmon production. This aspect of Atlantic salmon ecology is poorly understood.

A multi-scale framework for considering prey and Atlantic salmon production in streams

The importance of scale

Consideration of multi-scale constraints on ecosystem structure and function is an area of growing interest in stream ecology (e.g., Frissell et al. 1986; Rabeni and Sowa 1996; Poff 1997), and we suggest that a multi-scale perspective will be useful in assessing and predicting variation in Atlantic salmon production across the diverse landscapes that comprise its range. The physical structure of streams can be conveniently defined using a hierarchy of spatial scales (e.g., Frissell et al. 1986). Because environmental factors that limit either prey production or non-trophic habitat needs of Atlantic salmon operate at different scales, a focus on only one scale may result in a failure to identify limiting factors associated with another scale (see Rabeni and Sowa 1996).

Over its life span, the highly mobile, anadromous Atlantic salmon clearly experiences environmental and ecological factors occurring over a wide range of spatial and temporal scales (Folt et al. 1998). We focus on four of what we consider to be critical hierarchical spatial scales and then consider how selection of a particular scale of observation may influence perceptions of the importance of different factors that control Atlantic salmon production. Where possible, we also consider how these factors vary at different temporal scales, because temporal variability is a critical structuring force in running water ecosystems (Resh et al. 1988; Poff and Ward 1989, 1990; Townsend and Hildrew 1994; Poff et al. 1997).

The habitat hierarchy

Regional scale

At the regional scale, climate and biogeography are the most important factors that may regulate salmonid production. Climate determines thermal regime, amount and timing of runoff, and vegetation potential. Across the range of Atlantic salmon, clear regional differences in these climatic factors are evident (see Elliott et al. 1998). More northerly streams tend to have longer winters with extensive ice cover, and shorter, cooler summers than more southerly or northern maritime streams. The scouring effects of catastrophic ice breakup, for example, will be more pronounced in northern streams. Southern streams may have potential for higher invertebrate and salmon production because of a longer growing season. Warmer summer temperatures, however, may directly limit the growth potential of salmonids. Southern streams will also tend to have relatively less late-spring and summer discharge because of less precipitation storage as snow.

The role of biogeography in determining levels of production at the regional scale has received very little attention. The correlation between benthic invertebrate community composition and regional patterns of vegetation is well known (Ross 1963; Cummins et al. 1989); however, the influence that this relationship has on Atlantic salmon throughout a broad region that includes temperate hardwood forests, boreal coniferous forests, and taiga is unknown. Assuming that growth of juvenile Atlantic salmon is prey limited at times, regional factors that have strong bearing on food quality and quantity for invertebrates as well as the composition of prey communities may have subtle but probably significant effects on their production.

Watershed scale

Geology, vegetation cover, and land use are probably the major determinants of salmonid production at the watershed scale. Bedrock geology regulates the types and quantities of nutrients available for dissolution and also influences stream thermal regime. Streams draining watersheds with carbonate bedrock, for example, tend to have higher concentrations of dissolved ions and less variable thermal and hydrologic regimes, and support higher levels of total secondary production compared to streams draining other bedrock types (Krueger and Waters 1983; Huryn et al. 1995). Streams draining watersheds with deep glacial deposits also tend to have high thermal and hydrologic stability and may support higher levels of invertebrate production compared to streams draining watersheds with shallow soils (Krueger and Waters 1983). Watershed vegetation cover, land use and land-use history interact to influence secondary production in streams by numerous direct and indirect pathways, including hydrology, light, thermal regime, water chemistry, channel sediments and morphology (Freeman and Wallace 1984; O'Hop et al. 1985; Wallace and Gurtz 1986; Sallenave and Day 1991; Grubaugh and Wallace 1995; Sanchez and Hendricks 1997).

Reach scale

A stream reach is defined here as a length of stream channel that incorporates several local habitats. The distribution and abundance of local habitats are dictated by channel morphology and riparian conditions (Gregory et al. 1991). At the reach scale, stream width has long been identified as a central determinant of food quality and quantity, primarily because of its effect on the relative influence of riparian vegetation on stream energy budgets (Vannote et al. 1980). Habitat complexity also has important influences on reach-scale patterns of production by invertebrates (Huryn and Wallace 1987). Reaches that are constrained by bedrock will tend to

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have reduced habitat complexity and hyporheic volume, and faster through-flow of organic matter and nutrients compared to unconstrained, alluvial reaches (Gregory et al. 1991). Such reaches are predicted to have high proportions of low-productivity habitat (e.g., bedrock run and glide) and lower levels of invertebrate and fish production compared to unconstrained reaches (e.g., alluvial cobble-riffle). This relationship is poorly defined, however, and may become inverted, for invertebrates at least, in bedrock-constrained reaches with an abundant cover of aquatic mosses (Grubaugh et al. 1997). Reaches that are separated by selective barriers to fish movements, such as waterfalls or beaver dams, may show differences in fish community structure (Crowl et al. 1992; Schlosser 1995) that may effect levels of reach productivity because of cascading effects within food webs (Huryn 1998).

Local-habitat scale

Water depth, velocity, and type of substratum are often used to identify spatially distinct channel features designated here as local habitats (or channel unit habitats — Hawkins et al. 1993). Local-habitat type, such as riffle or pool, strongly influences the local distribution and abundance of aquatic fauna, both invertebrates (Huryn and Wallace 1987) and fish (Angermeier 1987; Schlosser 1991). Secondary production in high-gradient headwater streams tends to be relatively uniform among habitats, largely because of high levels of production in debris-dam pools (Huryn and Wallace 1987). In lower gradient streams with more mobile beds, however, riffle habitats are usually considerably more productive than pools (Fisher 1977; Bowlby and Roff 1986*a*; Grubaugh et al. 1997). Not only can habitat influence the production of prey biomass, but by influencing their community structure, this factor can also influence the relative availability of quality prey to drift feeding salmonids (Rader 1997).

Factors that determine prey production in Atlantic salmon streams

Secondary production is essentially the product of the growth rate and biomass of an animal population, and the numerous factors that determine production will generally operate upon these variables. There are available a number of excellent reviews of factors affecting growth and production of stream invertebrates (Resh and Rosenberg 1984; Benke 1993). Rather than providing a comprehensive treatment of all factors identified as significant in this regard, we attempt to highlight factors that may be significant for Atlantic salmon streams in particular.

Temperature

Temperature directly regulates rates of metabolism, growth, and development in stream invertebrates (Sweeney 1984). Atlantic salmon streams are largely restricted to the boreal or sub-boreal biomes, which are characterized by short summers and long, cold winters. Accordingly, P/B ratios are expected to be low in Atlantic salmon streams, due both to the short length of the growing season and to the relative dominance in these streams of invertebrate species that generally do not produce more than one generation per year (Clifford 1982; Jacobi and Benke 1991). At the watershed scale, bedrock geology, vegetative cover, and land use influence thermal regime, by regulating soil temperatures and the degree to which precipitation infiltrates into the soil and moves as groundwater to the stream. Large contributions of groundwater to stream discharge, for example, will moderate thermal extremes by buffering against cold winter conditions in northern regions or warm summer conditions in southern regions of the Atlantic salmon's range. Large-scale removal of forest cover due to clear cutting or row cropping, on the other hand, will enhance thermal extremes because of its effect on temperatures of soil and infiltrating precipitation. Thermal regimes are also influenced by reach-scale features, such as riparian cover or the relative proportion of deep pools that reduce rates of heat exchange with the atmosphere. Finally, variation in thermal regime among local habitats has been shown to influence spatial patterns of invertebrate growth rates and may therefore have consequences for prey production (Gresens 1997).

Food

Invertebrate growth rates are strongly influenced by food quality (Hill 1992) and quantity (Richardson 1991). The quality of food type is determined both directly and indirectly by vegetation cover, and this has important effects on the structure of prey communities for Atlantic salmon. The quality, quantity, and timing of input of terrestrial detritus to streams may vary considerably in quality at regional scales across the range of the Atlantic salmon (e.g., hardwood detritus in the south, softwood detritus in the north), with this variability being reflected by differences in community structure, life histories and probably production dynamics of resident macroinvertebrate populations (Ross 1963; Cummins et al. 1989). Latitudinal trends in vegetation will also effect water chemistry, with acidic streams — often characterized by low levels of invertebrate production (Krueger and Waters 1983) — being more widespread at higher latitudes. At more local scales, e.g., in locations approaching or exceeding the timberline (either high altitude or high latitude), or in wide and shallow rivers, the absence of canopy-forming vegetation may produce a change in primary energy source, from terrestrial detritus to algae, which will be correlated with changes in macroinvertebrate community structure and production (Wiggins and Mackay 1978; Vannote et al. 1980; Behmer and Hawkins 1986). Nutrient concentrations are also important determinants of food quality and quantity and will vary widely throughout the range of the Atlantic salmon depending on regional geology and watershed land-use. Limited information indicates that moderate levels of agricultural land-use actually enhance Atlantic salmon production because of associated inputs of nutrients to otherwise oligotrophic streams in Europe (Kennedy et al. 1983; Bergheim and Hesthagen 1990). Presumably this increase is due to bottom-up control of prey production (cf. Johnston et al. 1990; Peterson et al. 1993).

Disturbance

Although poorly studied, the effects of winter freezing and subsequent ice breakup on aquatic invertebrate production are probably particularly important regional-scale factors influencing the productivity of Atlantic salmon streams. Ice breakup and associated flooding, which has been shown to cause large increases of drifting insects and detritus in

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northern rivers, are likely a critical determinant of annual patterns of prey biomass and species composition (Hudon 1994). The effect on invertebrate production dynamics of floods not associated with ice breakup will be a function of hydrologic regime and substratum stability (Scarsbrook and Townsend 1993). The timing and frequency of floods relative to life cycle stage of the invertebrates (e.g., winter or summer, cf. Hudon 1994; Huryn et al. 1995) and the presence of channel refugia during floods (Scarsbrook and Townsend 1993; Palmer et al. 1996) can influence magnitude of biomass loss. Regional differences in climate and watershed or reach differences in sediment size and mobility will interact to influence the local importance of disturbance in any particular Atlantic salmon stream. In general, however, the fact that many invertebrates in north temperate and boreal streams require at least 1 year to complete their life cycles implies that recovery of biomass due to scouring floods will be slow, especially when contrasted with streams in regions having communities of invertebrates characterized by rapid growth rates and short life cycles (e.g., Fisher and Gray 1983). Accordingly, the reduction of invertebrate biomass by scouring floods, especially those associated with ice breakup (Hudon 1994), implies reduced food supply for Atlantic salmon on an annual scale. Understanding the effects of ice breakup is probably crucial to understanding long-term variability of production dynamics in Atlantic salmon streams.

Biotic interactions

Although poorly studied, regional invertebrate-species pools may influence the proportion of total prey production readily available to salmon. Wootton et al. (1996), for example, observed that the abundances of palatable prey species in California streams that support high growth rates in juvenile steelhead trout (*O. mykiss*) can be reduced by the presence of a caddisfly species (*Dicosmoecus*) that is invulnerable to predation. *Dicosmoecus*, along with other invulnerable invertebrates (e.g., aquatic moth larvae), tends to dominate in drought years when scouring floods are rare (Power 1992), suggesting that interannual variation in climate may indirectly influence production by steelhead trout via production dynamics of prey communities. The extent to which regional differences in dominant, invulnerable species may influence prey availability to Atlantic salmon (or other stream predators) and thus potentially limit salmon production is virtually unknown.

Regional patterns of the composition of fish assemblages may also have consequences for production by their invertebrate prey. Some invertivorous fish species, for example, may depress prey production directly by reducing prey biomass more effectively than others (Huryn 1998) or indirectly by affecting invertebrate feeding behavior (see below). Because of these differences in feeding behavior, different assemblages of fish will probably have different effects on their prey populations. Studies of how biogeography controls community interactions, and how these interactions may function to regulate secondary production over large areas will enhance understanding of factors contributing to variation in Atlantic salmon production at the regional scale.

On the local habitat-scale, interspecific competition (Hill 1992) and the non-lethal effects of predators (McPeek and Peckarsky 1998) have been shown to result in a decline in invertebrate growth rates. The effects of this latter factor are currently receiving a great deal of attention because, although subtle, they are clearly widespread and of substantive quantitative significance (McPeek and Peckarsky 1998). This is because avoidance behavior by benthic insects in response to their salmonid predators usually results in a reduction in time spent feeding, which may have consequences for rates of larval growth and development as well as fecundity of adults (Ball and Baker 1996; McPeek and Peckarsky 1998). A reduction in growth or feeding activity may ultimately affect levels of secondary production by prey populations and primary producers, which in turn may influence production dynamics of adjacent trophic levels (Flecker and Townsend 1994; McIntosh and Townsend 1995; 1996; Peckarsky and McIntosh 1998). It is important to note that although avoidance behavior by invertebrates operates at a relatively local scale (e.g., local habitat), factors that affect the distribution of their salmonid predators are probably controlled by factors operating at the reach, watershed, or regional scale (e.g., Crowl et al. 1992).

Terrestrial invertebrates

Although there have been many studies demonstrating that terrestrial invertebrates are consumed by stream fishes, only a handful have attempted to directly quantify the importance of this food source to fish production or to determine factors that influence quantities of terrestrial invertebrates that enter streams (Nelson 1965; Mason and Macdonald 1982; Edwards and Huryn 1995, 1996; Huryn 1996; Cloe and Garman 1996; Wipfli 1997). The most recent research has answered questions about how different riparian management activities influence terrestrial inputs to streams (Edwards and Huryn 1996) and how riparian zones might be modified to enhance this food source (Wipfli 1997). Edwards and Huryn (1996), for example, showed that salmonid streams in New Zealand with riparian zones with either forest or native grasses received significantly greater amounts of terrestrial invertebrates compared to streams bordered by pasture. Wipfli (1997) found that the species composition and successional stage of riparian vegetation along forested streams in Alaska can influence the availability of terrestrial invertebrates to juvenile coho salmon.

Non-trophic constraints on Atlantic salmon production

Close coupling between Atlantic salmon and prey production is not expected if factors other than prey production and availability have strong effects on salmonid growth or mortality (e.g., Gibson et al. 1993; Gotceitas and Godin 1993). The potential impact of such "non-trophic factors" on any particular population of Atlantic salmon, however, will depend on the availability of specific habitat types that promote growth and minimize mortality over the freshwater period of the salmon life cycle. Here, we briefly consider a number of non-foraging habitat types thought to be critical to Atlantic salmon production. Assessment of the relative importance and how the availability of these critical habitats may change across the range of Atlantic salmon is necessary for understanding spatial variation in Atlantic salmon production.

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Spawning and summer feeding habitat

Adult salmon construct redds in small streams providing erosional areas with moderate velocities and depths and with unarmored and porous substrata (see Gibson 1993). Lack of available spawning habitat (at the local-habitat, reach, or watershed scale) will obviously limit salmon production (see Gee et al. 1978). After emergence from the redd, fry generally disperse but remain within riffles to forage during the spring and summer. Some age-class segregation among parr occurs because, as juveniles grow, they tend to move into slightly deeper, faster water with coarse substrata.

Atlantic salmon generally require water temperatures <20°C for positive growth. In more southerly latitudes, these temperatures may be exceeded during summer. Gibson (1988) observed juvenile salmon in pools but not riffles at temperatures of 24°C, suggesting reduced growth potential. In some streams, groundwater sources may be a critical factor in maintaining suitable thermal habitat for salmonids (cf. Meisner et al. 1988). Indeed, survival of juvenile salmon in a Maine river has been positively associated with summer discharge. Adequate levels of discharge are apparently required to maintain both cooler temperatures and available feeding habitat (Havey and Davis 1970).

Overwintering habitat

As water temperatures cool in the autumn, juvenile salmon move into sheltered habitats to overwinter. Parr may hide under large substrata in runs and riffles (Gibson 1978; Cunjak 1988), or to move into deep pools (Allen 1940; Jensen and Johnsen 1986), or show both behaviors (Cunjak 1996). The availability of sheltered winter habitat is probably most critical in streams with extensive ice cover, which reduces total habitat volume and can cause high parr mortality during ice breakup. Mortality risk may vary with reach-scale habitat structure and from year-to-year. For example, in years when ice breakup occurs slowly, stream riffles tend to be more heavily scoured than pools; however, in years of dynamic, rapid breakup, all habitat types tend to be scoured (R.A. Cunjak, Dept. Fish. and Oceans, personal communication). In some watersheds, local groundwater inflows may serve to maintain important open-water refuges during winter (Cunjak 1996). The potential significance of winter conditions to production is revealed in comparative studies. Randall and Paim (1982) reported that salmon production tended to be lowest in streams where ice cover and near 0°C temperatures occur for about 6 months every year (e.g., New Brunswick, northern Norway). The highest levels of production were recorded from streams where near-zero temperatures occur for <2 months of the year (e.g., Egglishaw 1970). These differences were attributed to lower biomass and, to a lesser extent, slower rates of growth in the colder streams (Randall and Paim 1982). This conclusion suggests that biomass losses caused by winter mortality should be suspected as an important mechanism controlling patterns of production at watershed and regional scales.

Refugia from predation and competition

Although juvenile salmon apparently prefer riffle habitat in the summer, they may frequent pools when potential competitors and predators are absent. There is also some evidence that parr growth rates may actually be higher in pools (see Gibson 1993). Whether avoidance of pools by parr is due to relatively poor competitive ability compared to other species (cf. Fausch 1998) or due to vigilance against potential predators (e.g., adult brown trout, kingfishers) is not known. It has been shown experimentally, however, that juvenile Atlantic salmon exposed to model rainbow trout or stuffed kingfishers show reduced foraging activity (Metcalfe et al. 1987; Gotceitas and Godin 1993).

Refugia from high flow

Spates may reduce salmon production through several mechanisms. Spates that occur prior to fry emergence can scour redds and cause egg or alevin mortality. This is probably of more concern in watersheds where some autumn and winter precipitation falls as rain (e.g., in southern end of range or coastal streams — see Elliott et al. 1998). Large rain-on-snow events can be particularly devastating if they cause redds to be scoured, as has been shown for fall-spawning salmonids in the California Sierra-Nevada (Erman et al. 1988). At the watershed scale, human activity that elevates sediment loads in streams may also increase the effective scour depth for a given discharge, thus reducing egg/alevin survival (Montgomery et al. 1996).

Spates that occur after dispersal from the redds can also cause mortality of young salmon. Juvenile fish in general are vulnerable to downstream displacement by floods (e.g., Harvey 1987). Environmental factors that mitigate mortality from floods include stable large woody-debris (Moore and Gregory 1988; Pearsons et al. 1992) or streambed structure that provides hydraulic dead zones during high water (Lancaster and Hildrew 1993).

Predicting invertebrate and Atlantic salmon production at multiple scales

Clearly, the empirical data do not exist to allow us to rigorously demonstrate the details of how a multi-scale framework operates to control production of juvenile Atlantic salmon. Nonetheless, we believe an attempt to organize existing information in a hierarchical context will aid in identifying important knowledge strengths and gaps that suggest critical research areas that could help define limits to Atlantic salmon production across its enormous range. In keeping with the spirit of the workshop that spawned this paper, we attempt to make some predictions about expected patterns of invertebrate and salmon production at different habitat scales. We view these predictions as critical uncertainties, which, if answered, would greatly increase our understanding of fish–habitat relations and thus contribute to Atlantic salmon conservation, restoration, and management.

General prediction

Larger-scale factors can override factors controlling salmon production at smaller scales

This general prediction is central to a hierarchical view of habitat constraints on ecosystem productivity. For example, water chemistry, water temperature, and sediment supply, important determinants of the biological characteristics of streams, are largely controlled by watershed-scale processes. These factors interact to exert strong control on habitat

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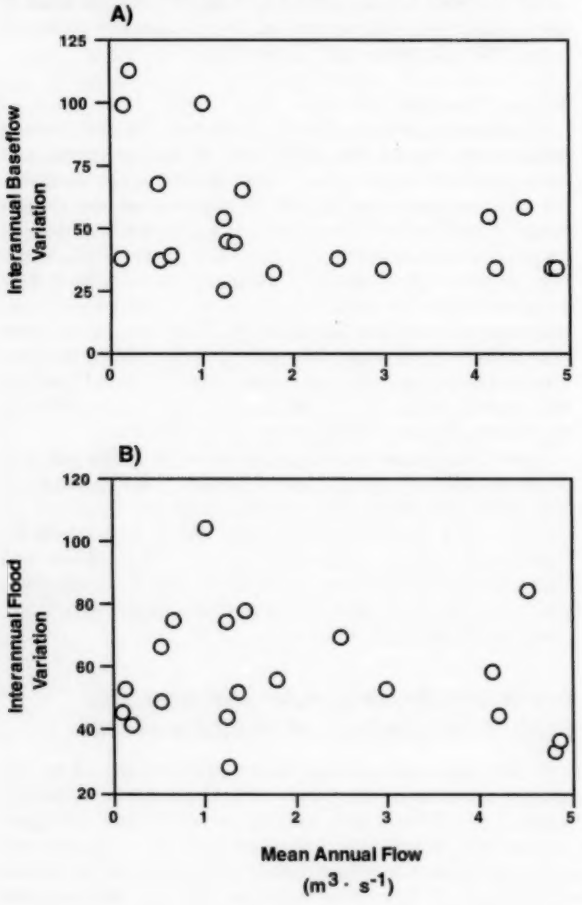
Fig. 2. Relationship between stream size (mean annual flow) and (*a*) interannual baseflow variation (coefficient of variation in the ratio of annual low flow to mean annual flow) and (*b*) interannual flood variation (coefficient of variation in magnitude) for 20 unregulated streams in New England (U.S.A.).



complexity and stream productivity at the reach scale. Similarly, reach-scale factors, such as riparian conditions or channel width, influence productivity at the local habitat scale by regulating the supply of terrestrial vs. instream carbon sources. Understanding of watershed to local habitat-scale processes occurring within the range of the Atlantic salmon is crucial for effective restoration and management of streams because effort can then be focused on the hierarchical scale(s) that will provide the most effective response. Given the importance of the general prediction of top-down control within a habitat hierarchy, however, it is significant to note that some mitigation procedures, such as use of riparian buffer zones to reduce sediment or nutrient inputs to streams, are actually attempts to invert the habitat hierarchy by reducing the effect of a higher-order factor (e.g., watershed) by modifying a lower-order factor (e.g., reach). However, the efficacy of small-scale remediation in a setting of larger-scale watershed perturbation may be limited (see Frissell and Nawa 1992; Roth et al. 1996; Allan et al. 1997).

Watershed scale predictions

Hydrologic regime will be a determinant of salmon production

Hydrologic extremes, in particular, may serve as surrogates for habitat quantity and perhaps quality, and thus be useful in predicting differences in production among salmon streams (cf. Poff and Ward 1989). Streams with stable baseflows will have high relative thermal stability, to be less prone to drying, especially during summer, and to have a favorable chemistry (alkalinity, pH) that supports greater invertebrate and salmonid production (Krueger and Waters 1983; Kwak and Waters 1997). Figure 2*a* shows for 20 streams in New England, U.S.A. (from Poff 1996) that the interannual variability in baseflow stability (a measure of how low streamflow drops relative to the mean annual flow) varies substantially, especially for small streams $<2\ m^3 \cdot s^{-1}$. Providing that sediment supply is sufficient to maintain spawning habitat, streams with lower variability in baseflow stability may be expected to afford more favorable habitat for salmon production. In a similar vein, interannual variability in the magnitude of high water conditions may also indirectly assay risk to juvenile salmonids during the few to several years they reside in a nursery stream. For the same 20 small New England streams, the range of variability in high flow conditions varies by a factor of two, suggesting some streams may provide more temporally benign environments (and potentially higher production) than others (Fig. 2*b*). Interestingly, these variables (baseflow stability and high flow variability) are not strongly correlated for these 20 streams ($r = 0.37$), suggesting that many of these streams may have different hydrologic constraints.

Land use will be a determinant of salmon production

Land use activities at the watershed scale that enhance sediment input and thermal extremes of streams, such as large-scale clear cutting, row cropping, or construction, will have a negative effect on Atlantic salmon both indirectly by influencing prey production and directly by influencing fish mortality. For example, input of silt to a Minnesota stream from residential construction and agricultural activity in its upper watershed caused decreases in annual invertebrate production over a 5-year period (Waters 1982). Variation of brook trout (*Salvelinus fontinalis*) production followed an identical trend. This covariation was attributed either to food limitation of trout or to the negative effects of siltation on survivorship of both invertebrates and trout eggs and alevin (Waters 1982). Recent work in Michigan has demonstrated that the intensity of watershed-scale agricultural activity is much more important in explaining site-to-site variation in stream indices of local habitat and biotic integrity than is local riparian condition (Roth et al. 1996; Allan et al. 1997). Moderate amounts of agricultural land-use, however, have been shown to have a positive effect on Atlantic salmon production, presumably due to enhancement of the trophic basis for prey production in nutrient-poor watersheds (Kennedy et al. 1983; Bergheim and Hesthagen 1990; see also Johnston et al. 1990; Peterson et al. 1993).

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Fig. 3. Hypothetical curves showing a linear (A) or threshold (B) response of juvenile salmon production to percentage of alluviated stream reaches at the watershed scale.

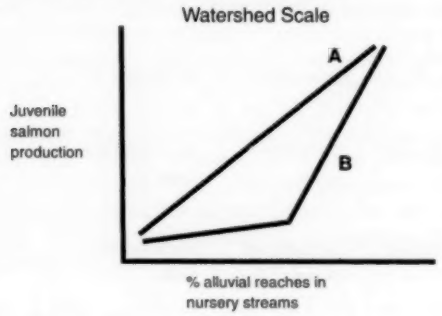
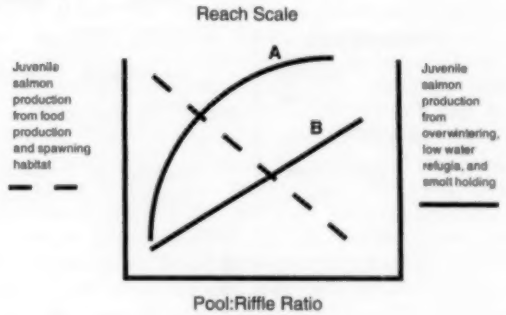


Fig. 4. Hypothetical curves relating juvenile salmon production to stream the percentage of riffles and pools at the reach scale. Viewing the contribution of pools to production as non-linear (A) or linear (B) determines the optimum habitat configuration that supports maximum salmon production (points where the lines cross).


Reach Scale
Juvenile salmon production from food production and spawning habitat
A
B
Juvenile salmon production from overwintering, low water refugia, and smolt holding
Pool:Riffle Ratio

Composite reach-structure will be a determinant of salmon production

Factors likely to regulate total production potential for salmon at the watershed scale include the proportion of alluvial stream reaches, which provide both high quality food and non-foraging habitats. The degree to which salmon production may increase with alluviation, however, is not at all clear: production may increase relatively steadily with percent alluvial reaches (Fig. 3, line A), or it may remain relative flat until some threshold is passed (Fig. 3, line B). Clearly, the distinction would be important in terms of identifying suitable watersheds for Atlantic salmon restoration. Additionally, the spatial and temporal *connectivity* of stream reaches is critical to allow salmon to discover and exploit optimal habitat at the watershed scale. Selective barriers that restrict movement between reaches can greatly influence spatial patterns of salmon distribution and production. The effects of man-made barriers (e.g., dams) as barriers to efficient movement is well documented; however, the natural structures (e.g., waterfalls, beaver dams) at the local or reach scale can also exert a strong influence over watershed-level production (cf. Crowl et al. 1992; Schlosser 1995).

Reach scale predictions

Proportion of trophic and non-trophic habitat will be a determinant of salmon production

Maximum salmon production should occur under an optimal combination of trophic and non-trophic habitat types. For example, the relative availability of riffles and pools almost certainly influences salmon production. Bowlby and Roff (1986*b*) found that maximum biomass of multi-species salmonid assemblages sampled from 30 m long reaches in southern Ontario streams peaked at about 44% pool area. For Atlantic salmon, riffles are critical habitat for providing quality prey production and for spawning habitat, whereas pools serve important non-trophic functions, such as overwintering (Cunjak 1996), summer low flow refugia (Gibson 1988), or holding areas for smolts (R.A. Cunjak, Dept. Fish. and Oceans, personal communication). However, the frequency and (or) diversity of the various habitat types needed to maximize Atlantic salmon production is unknown (Gibson 1993; Cunjak 1996). Trophic habitat probably declines with increasing frequency of pools, but the degree to which the non-trophic function of pool habitat will contribute to potential salmon production is unknown. As an illustration, relatively few pools may be needed to ensure high survival of juveniles (Fig. 4, line A), or survival and subsequent production may increase relatively linearly with pool availability (Fig. 4, line B). In this hypothetical example, the fewer pools needed to ensure survival during bottleneck periods, the greater the potential salmon production in the reach. The slopes of these hypothetical curves might be expected to change as environmental conditions change, e.g., siltation (a watershed factor) would drive the food-production line down. Although this example is clearly an oversimplification of reality, it points to important potential tradeoff that needs some quantification if we are to understand geographic variation in limits to salmon production.

Non-trophic habitat requirements may cause uncoupling of prey – salmon production relationships

Depending on the interaction between non-trophic and trophic habitat requirements, the extent to which salmon are food-limited will vary with habitat structure. For example, in Fig. 4, the points of intersection of lines A and B indicate when limits on "carrying capacity" switch from food-limitation to non-food limitation. Until more is known about the interaction between non-trophic and trophic habitat requirements, the degree to which juvenile salmon production is coupled to invertebrate production will remain obscure.

Local habitat-scale predictions

Availability of specific local-habitat types will control prey community composition and production

Although this factor has received a great deal of study in temperate streams, there is little information about habitat–production relationships for prey communities in high latitude streams. The lack of this information renders recommendations about local-habitat types most favorable for salmon foraging speculative. Relative levels of prey production in pool versus riffle or bedrock outcrop in Atlantic salmon streams, for example, are for the most part unknown.

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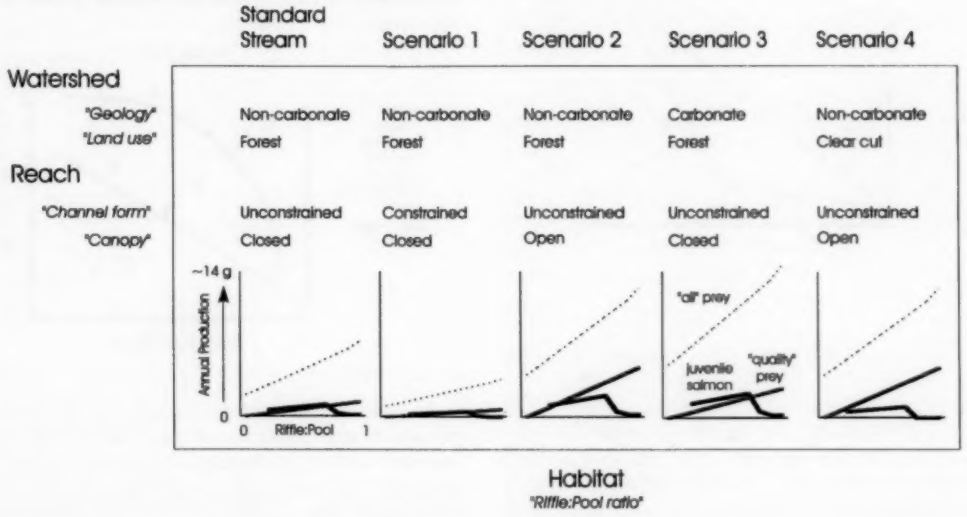
Fig. 5. A multi-scale view of selected factors suspected to influence secondary production in Atlantic salmon streams. The four quantitative scenarios presented in this figure are purely hypothetical, yet constrained to occur within realistic limits. These scenarios compare a hypothetical "standard stream" (left graph in all scenarios) to others that are influenced by factors operating at different levels within a spatial hierarchy (habitat, reach, watershed). See text for further explanation.



Production of quality prey is a determinant of salmon production

Prey – salmon production relationships based on measurements of gross prey production may obscure coupling between trophic levels, should these exist. Salmon production may be more profitably evaluated against the availability of high quality prey, both benthic (cf. Rader 1997) and terrestrial. Although processes operating at the reach scale will influence total prey quantity (e.g., proportion of trophic habitat available across the reach), the specific types of local habitat present will determine the production of quality prey for Atlantic salmon, because of the fundamental relationship between local habitat and invertebrate community composition.

A synthesis

An attempt to integrate selected physicochemical and non-trophic habitat limitations on invertebrate and salmon production in a multi-scale context is presented in Fig. 5. We provide these graphs as an heuristic device to show the value of conducting detailed production studies in a multi-scale framework and to highlight knowledge gaps about factors influencing production in salmon streams. Since comprehensive data do not exist, these quantitative scenarios are hypothetical, yet constrained to occur within realistic limits. The graphs predict how production of invertebrates and salmon respond to factors operating at three spatial scales: watershed, reach, and local habitat. An hypothetical "standard stream" of specified watershed and reach characteristics is used as a basis for comparing scale-dependent responses. Composite local habitat-scale effects are represented by a changing ratio of riffle to pool area; reach-scale effects are represented by contrasts in channel constraint and riparian-canopy cover; watershed-scale effects are represented by contrasts in bedrock geology (non-carbonate versus carbonate) and land use (hardwood forest versus clearcut).

Our "standard stream" has an alluvial riffle-pool channel with a closed forest-canopy; riffles have coarse substrata and pools have fine sediments and are scoured during high flows; the watershed is forested and the bedrock is non-carbonate material. The composite local habitat ranges from 100% pool (extreme left of the X-axis on all graphs) to 100% riffle (extreme right). The Y-axis indicates hypothetical levels of habitat-weighted production expected for total benthic invertebrate prey, quality prey (sensu Rader 1997), and juvenile Atlantic salmon. Annual invertebrate production in riffles (7 g AFDM $\cdot$ m^{-2}) and pools (2 g AFDM $\cdot$ m^{-2}), and ratio of riffle to pool production (3.5) are based on reports for temperate streams with alluvial channels and mean discharge ~1 m^{-3} $\cdot$ s^{-1} (e.g., Benke 1993; Grubaugh et al. 1997). The proportion of production attributable to "quality prey" was set at 20% of riffle production, which is probably liberal for forested streams (cf. Huryn and Wallace 1987). Gross production efficiency of juvenile salmon was set at 20% for non-quality prey and 25% for quality prey. There is fairly good evidence to support the former efficiency (Waters 1988), but little evidence to support the latter, which may be conservative. Salmon were assumed capable of consuming all prey. Salmon production was assumed to be zero until pool habitat was reduced to less than 90% of the total stream area due to lack of sufficient riffle habitat for spawning. Once the pool habitat decreased to below 30% of the stream area, salmon production was reduced to reflect other non-trophic habitat limitation. There is no empirical basis for a precise threshold response as indicated on the graphs (cf. Fig. 4), so salmon production was simply decreased in proportion to the ratio of decreasing pool area to increasing riffle area. To examine how invertebrate and fish production respond to environmental factors at different hierarchical

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scales, we manipulated reach-scale features (Scenarios 1 and 2) and watershed-scale features (Scenarios 3 and 4).

Scenario 1. The standard unconstrained alluvial reach is compared to a bedrock constrained reach in a forested, non-carbonate watershed. Annual macroinvertebrate production on the bedrock run habitat was set at 3.5 g AFDM · m^{-2}, and production in pools was set at 1 g AFDM · m^{-2}, or 50% of the production expected for alluvial riffle and pool habitats in similar size streams, a conservative difference assuming no moss cover (Purvis 1995). Salmon production was also reduced by 10% to reflect greater bioenergetic costs associated with foraging and maintaining position in this low-cover stream channel.

Scenario 2. The canopy has been removed from the standard stream, but the watershed remains forested beyond the channel margins. Production in riffles is increased 1.7× relative to the standard stream, following Behmer and Hawkins (1986), who showed a ratio of production in open riffles to shaded riffles ranging from 0.6 for filter-feeders to 2.8 for collector-gatherers and facultative grazers. Production in pools was increased 2× to reflect an overall increase in production because of enhanced quality of algal-derived detritus. The proportion of quality prey in the riffle habitat was doubled to 40% of total prey production, assuming a dramatic response of *Baetis* production after canopy removal (see Behmer and Hawkins 1986; Wallace and Gurtz 1986).

Scenario 3. The standard stream is modified to reflect a watershed-scale change in underlying geology of carbonate bedrock. Production in riffles and pools was increased 2×, which conservatively follows trends reported in the literature (Krueger and Waters 1983; Purvis 1995). However, Although quality prey production also doubled, its proportion was not increased beyond the standard 20%, because significant amounts of production in carbonate streams are often in the form of armored organisms, such as snails (Huryn et al. 1995; Purvis 1995). We note, however, that amphipods can be abundant in some carbonate streams (e.g., Krueger and Waters 1983). In such cases, the proportion of quality prey as amphipod production might be more substantial in these streams.

Scenario 4. In this scenario, the standard non-carbonate watershed has been clearcut, which also causes opening of the canopy at the reach scale. Invertebrate production was increased in riffles (1.7×) and pools (2×) reflecting the positive effects of increased light, temperature, and nutrients. The proportion of quality prey was also increased to 40% of riffle production to reflect expected increases in baetids (see Scenario 2). Unlike Scenario 2, however, salmon production was reduced by 50% to reflect the negative effects of clear cutting on thermal regime and silt deposition on egg and alevin survival.

Results. In each scenario, maximum annual salmon production occurred when riffle area comprised 70% of total stream area. In the standard stream, peak salmon production was 1.2 g AFDM · m^{-2}. Predictions of salmon production responded strongly to various scenarios of habitat alteration. Maximum annual salmon increased substantially when underlying geology was changed at the watershed scale to carbonate bedrock (2.4 g AFDM · m^{-2} in Scenario 3) and when canopy conditions were opened at the reach scale (2.1 g AFDM · m^{-2} in Scenario 2). Minimum salmon production was predicted when reach-scale channel form was constrained bedrock (0.5 g AFDM · m^{-2} in Scenario 1). In Scenario 4, where both watershed-scale and reach-scale factors were modified, predicted annual salmon production was 1.0 g AFDM · m^{-2}, a value similar to the standard stream. The range of predicted values falls within the range reported for Atlantic salmon streams, ca. 0.2–1.6 g · m^{-2}, with 3.1 g AFDM · m^{-2} being an extreme value from a carbonate watershed (Mann 1971). Certainly, the realism of these empirically based predictions about invertebrate and salmon production is questionable, given the gross assumptions and the extreme paucity of empirical data. Further, these predictions are based on short-term biotic responses to habitat alteration, and they do not take into account long-term geomorphic and ecological adjustments to habitat alteration. For example, while opening the canopy may stimulate short-term production of prey, removal of riparian trees can also result in a reduction of woody debris inputs to the stream channel. Subsequently, channel form may become simplified over time, resulting in reduced habitat complexity which can diminish cover for fish and may depress invertebrate production (see Gregory et al. 1991). Similarly, the prediction that clearcut watersheds with riparian canopy removal (Scenario 4) may produce as much salmon as the undisturbed standard stream does not take into account long-term habitat simplication, such as the reduction in pool frequency and size from siltation and loss of woody debris inputs (Bisson et al. 1992).

Despite these shortcomings, the scenarios are instructive because they allow us to visualize limitations to our knowledge about how multi-scale factors effect secondary production in streams. While the relationship between local habitat and production of stream invertebrates is firmly established, knowledge about how production might be influenced by factors operating at other spatial and temporal scales in the reach-watershed-region hierarchy are speculative. The scenarios do, however, allow us to posit several scale-dependent predictions that are relevant to both our earlier speculations (see "Predicting invertebrate and Atlantic salmon production at multiple scales," above) and to current and future research on Atlantic salmon (e.g., Armstrong et al. 1998; Parrish et al. 1998).

Conclusions

Our ability to predict how multi-scale factors might influence the productivity of Atlantic salmon streams is clearly limited given the present state of stream ecology. This lack of knowledge about multi-scale factors is largely attributable to the traditionally selected unit of study: the local habitat. As a consequence, the relationship between invertebrate production and local habitat is fairly well understood for temperate latitude streams, while understanding of factors operating above the scale of the local habitat for streams at any latitude are based largely on speculation. Compared to the relatively detailed knowledge about invertebrate production, there seems to be little general understanding about

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how trophic vs. non-trophic habitat influences salmon production at any scale. A predictive knowledge about salmon production across the geographic range of *Salmo salar* will require us to understand more clearly the dynamics of the relationship between trophic vs. non-trophic habitats and to define how this relationship changes with spatial scale — from local habitat on up the hierarchy.

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Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales

Kurt D. Fausch

Abstract: A review of 17 controlled experiments of interspecific competition between juveniles of Atlantic salmon (*Salmo salar*) and other fishes revealed relatively little evidence to judge competitive effects at any scale. More than half were unreplicated and so inadequate to test either the existence or relative strength of interspecific competition. Most replicated experiments used one of two designs appropriate to address questions of interest, such as whether nonnative species affect Atlantic salmon via competition or whether interspecific competition from coevolved salmonids is greater than intraspecific competition. Replicated experiments spanned a broad range of spatial and temporal scales, and one well-designed field experiment yielded the strongest inference at useful scales. Nonnative salmonids being introduced worldwide into Atlantic salmon waters have the potential to invade, so experiments testing their effects are most urgently needed. Overall, juvenile coho salmon (*Oncorhynchus kisutch*) are suspected to have the greatest effect, partly due to their inherent size advantage. The potential for complex interactions or indirect effects to modify effects of nonnative species is completely unknown but may be important and needs investigation.

Résumé : L'analyse de 17 expériences contrôlées de compétition interspécifique entre des saumons de l'Atlantique (*Salmo salar*) juvéniles et d'autres poissons n'a produit que peu de données permettant de juger des effets compétitifs à une échelle quelconque. Plus de la moitié des expériences n'étaient pas répétées, et ne permettaient donc pas de vérifier l'existence d'une compétition interspécifique ou sa force relative. Presque toutes les expériences répétées utilisaient l'une des deux approches d'adresser aux questions pertinentes, comme l'influence éventuelle des espèces non indigènes sur le saumon atlantique par la compétition, ou l'importance relative de la compétition interspécifique entre des salmonidés qui ont évolué ensemble et de la compétition intraspécifique. Les expériences répétées couvraient une vaste plage d'échelles spatio-temporelles, et une expérience de terrain bien conçue a permis d'obtenir la plus forte inférence à des échelles utiles. Comme les salmonidés non indigènes sont introduits partout dans le monde dans les eaux à saumon atlantique, qu'ils peuvent les envahir, il est impératif d'élaborer des expériences visant à déterminer leurs effets. En général, les cohos (*Oncorhynchus kisutch*) juvéniles auraient la plus grande influence, en partie à cause de l'avantage inhérent à leur taille. La possibilité que des interactions complexes ou des effets indirects modifient l'impact des espèces non indigènes est encore inconnue, mais elle peut être importante et doit être étudiée.

[Traduit par la Rédaction]

Introduction

Interspecific competition may be an important factor affecting growth and survival of Atlantic salmon (*Salmo salar*) during their juvenile life history in streams. During this freshwater phase Atlantic salmon throughout much of their range are typically part of simple assemblages consisting of only a few fish species. A subset of these, often only one other salmonid, make up a guild that feed on a common resource of drifting invertebrates. Members of such small guilds that exploit single resources are potentially strong interactors (Connell 1975; Paine 1992; Power et al. 1996), and therefore good candidates for showing ecologically significant effects from biotic interactions such as interspecific competition (Wiens 1989). Moreover, salmonids are known to respond quickly when resources or other species are added or removed (Chapman and Bjornn 1969; Fausch and White 1986), increasing the chances that niche shifts from such changes will occur, have important effects on fitness, and be detectable by experiments or observations.

In addition to the potential salmonid competitors with which Atlantic salmon coevolved, intentional and unanticipated introductions are increasing the chances that nonnative competitors, salmonids or otherwise, will become established in Atlantic salmon waters (Fausch 1988; Harache 1992). Increasingly, researchers and managers are being asked to predict effects of both native and nonnative competitors on Atlantic salmon stocks at a variety of scales and will need a sophisticated understanding to do so.

The purpose of this paper is to evaluate the evidence that native and nonnative interspecific competitors have strong direct effects on Atlantic salmon. Because in my view such data are largely inadequate at present, I begin by considering relevant scales of investigation and describing appropriate study designs for measuring such effects, in order to provide a template against which to measure the available evidence. After reviewing the relevant research to date, I briefly address more complex interactions such as condition-specific

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K.D. Fausch. Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, U.S.A.
e-mail:kurtf@cnr.colostate.edu

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competition and the potential for indirect effects through food webs and conclude by presenting my views about the most important effects to understand first. I deal here exclusively with interspecific interactions during the freshwater life stage from alevin to smolt, as others in this volume will treat potential competition during spawning (Fleming 1998), interactions between wild and stocked Atlantic salmon (Youngson and Verspoor 1998), and the population dynamics of intraspecific competition (Grant et al. 1998; Kocik and Ferreri 1998).

On scale

At what scale do we understand interspecific competition involving Atlantic salmon, and can knowledge at this scale address important ecological and management questions? This issue is challenging because although interspecific competition occurs moment-to-moment between individual fish by behavioral interactions, it is suspected to have wide-ranging and long-lasting effects on survival and fitness (Connor and Bowers 1987). How can we understand a phenomenon that affects organisms over such a wide range of scales? Here I address this problem by posing four questions.

First, what axes of scale are relevant to the study of biotic interactions like interspecific competition? I consider four — space, time, biological response, and biological organization. All are hierarchical, and should ideally be considered in the context of the life history of the organism studied (Wiens 1989). Thus, relevant spatial scales include individual home ranges, nested within local habitat patches occupied by many individuals, nested within a region that may contain many local patches that support a population linked by dispersal, all within the biogeographic scale that encompasses the entire species range. Stream ecologists also view stream habitat in a similar nested spatial hierarchy, from microhabitats nested within individual habitat units (riffles, pools, etc.), to stream reaches, sub-basins, and finally entire drainage basins (Frissell et al. 1986; Poff 1997). How individual and population processes scale to these physical habitat units will determine the physical dimensions of study designs needed to answer specific questions (Wiens 1989; Wiens et al. 1986). Similarly, the temporal scale relevant for understanding ecological processes can be viewed within a hierarchy ranging from daily and seasonal cycles to annual breeding cycles and mean generation times.

Also important for studying interspecific competition are hierarchical scales of biological response and biological organization. Thus, biological responses to competitors can be measured as changes in behavior, physiology, growth, survival, and fitness (Fausch 1988), each of which may answer a different question about the effects of competition on individuals or populations. Finally, interspecific competition can be measured at different levels of biological organization, those of interest for Atlantic salmon usually being individuals, populations, and perhaps metapopulations.

A second question, which gets at the importance of considering scale, is whether answers about interspecific competition change across scales. For example, might intense behavioral interactions at the individual level nevertheless have little effect on survival and fitness at the population level over the long run? Welden and Slauson (1986) distinguish between the *intensity* of competition, referring to its proximate behavioral or physiological effects on individuals, versus its *importance*, the ecological and evolutionary consequences of those effects relative to all other biotic and abiotic factors. To use a specific example, if limited stream habitat produces strong density-dependent juvenile mortality over winter (e.g., Mason 1976), then above some threshold reduced survival during the previous summer due to strong interspecific competition with another salmonid might have little effect on smolt output and long-term population viability. Thus, one might predict intense interspecific competition between juveniles during summer to be more important where winter conditions are benign and habitat abundant, than where they are harsh and limiting.

These considerations lead to a third question. What are relevant scales along the four axes for studying interspecific competition involving Atlantic salmon? The answer requires striking a balance between asking meaningful questions versus designing experiments that can detect a response. For example, for managers charged with maintaining viable populations of Atlantic salmon, it would be most appropriate to measure survival at the local habitat patch scale over annual time increments (relevant periods for survival of emerging fry would be less), to understand effects of interspecific competitors on local populations (cf. Wiens 1989). I hasten to add however, that the intensity of competition is likely to vary annually and by location, making it necessary to consider other evidence at a variety of scales, from individual behavior and growth to zoogeographic distributions, to place the results of such experiments in an appropriate context (Bender et al. 1984; Wiens 1989).

Because much study of interspecific competition among salmonids has been done at the scale of individuals in laboratory streams (e.g., Griffith 1972), a final question is what evidence we have about its effects at the population level in local habitats over annual increments. I address this in the analysis below.

On testing competition

Before analyzing specific tests with Atlantic salmon, it is appropriate to first define interspecific competition and place it in context among other factors that influence guilds of drift-feeding salmonids. Here I follow Wiens (1989) who defines interspecific competition as an interaction between members of two or more species that, as a consequence of either exploitation of a shared resource or interference related to that resource, has a negative effect on fitness-related characteristics (e.g., growth, fecundity, survival) of at least one species. The interspecific interference displayed by stream salmonids for favorable feeding locations from which to capture drifting invertebrates satisfies many of the criteria needed to clearly demonstrate at least the existence of interspecific competition (Reynoldson and Bellamy 1971; Wiens 1989), such as that species overlap in resource use, intraspecific competition occurs, and resources are limiting. The high natality of fishes, coupled with a seasonal environment where space and invertebrate drift resources decline drastically each year in many systems, ensures that resources will be limited resulting in high intraspecific (e.g., Grant and

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Kramer 1990) and interspecific competition. This, in turn, leads to a "critical period" or bottleneck for juvenile survival (Elliott 1994), a feature common to many fishes (LeCren 1965). Moreover, such bottlenecks are generally predictable year to year, because even a relatively low density of adults can saturate the available habitat with progeny (see Ricker 1954; Elliott 1994 for examples).

Despite the primacy of interspecific competition in past explanations of community patterns (see Ross 1986 for a review), it is important to place it in an appropriate context among other factors that affect distribution and abundance of salmon. Although biotic interactions like competition and predation may have strong effects at individual to population scales, species-specific responses to environmental factors set the template upon which those biotic interactions work (Poff 1997). Simply put, these concepts are identical to the fundamental niche (species-specific response to the environment) and realized niche (considered broadly, the niche after including effects of all biotic interactions) of Hutchinson (1957). Similarly, legacies due to history and chance, coupled with lag times after disturbances, often form an even broader template of habitat heterogeneity across landscapes upon which species array themselves according to their fundamental and realized niches. It is wise therefore, to consider that the potential for interspecific competition will be determined by autecology that controls whether species will co-occur at all, as well as the spatial and temporal heterogeneity of habitat and other physical conditions which may modify its outcome (Dunson and Travis 1991).

Experimental design

Assuming that appropriate scales of space, time, and biological response and organization have been selected that are suited to the question of interest, the next issue is how to design an experiment to rigorously test interspecific competition. Appropriate designs will subsequently be used here to assess whether studies to date have yielded strong inferences about competition between Atlantic salmon and other fishes. Before turning to designs, however, I first address the basic theory of population dynamics under interspecific competition.

The Lotka–Volterra competition equations provide a formal mathematical theory long used by ecologists to predict population growth rate of one species from its own abundance and that of one or more competitors (reviewed by Law and Watkinson 1989). Considering a simple community with only two competing species, experiments that manipulate the abundance of each using either single short-term (i.e., "pulse") or sustained ("press") manipulations (Bender et al. 1984), can be employed to estimate the two competition coefficients, basic parameters needed for these equations. The competition coefficients measure the effect on population growth rate of one interspecific competitor relative to the effect of one intraspecific competitor. However, although these coefficients have been successfully measured in the laboratory for organisms like *Drosophila* with simple life cycles, the required field manipulations are logistically impossible for large mobile organisms with complex life histories. Moreover, the theory has proved too simple (Law and Watkinson 1989). Vertebrate populations may not follow Lotka–Volterra dynamics, because competition coefficients may depend on density or environmental conditions and do not account for age or size structure of populations. After an extensive review, Law and Watkinson (1989) concluded that despite the formal theory, the basic underpinning of empirical field data on interaction strengths needed to adequately test it is lacking. For that reason, I focus here on experimental designs to empirically test such interaction strengths for a mobile vertebrate with a complex life cycle, such as Atlantic salmon.

Two other issues known to most fish ecologists are also important to review before discussing designs. First, it is fundamental that experiments at any scale must be properly controlled, replicated (not pseudoreplicated *sensu* Hurlbert 1984; Underwood 1986, 1997), and randomized. Controls allow separating effects of the added competitor from other disturbances caused by experimental manipulations (e.g., electrofishing and handling), replicates allow separating effects of the competitor from differences among sites used for controls and treatments, and randomization of replicates to treatments and controls avoids bias that might affect results. Second, experiments must be designed with care to closely mimic the natural environment that provides the arena for competition, to minimize disturbances other than adding the competitor, and to control for any other disturbances. Otherwise, the hypothesis being tested by the experiment may be fundamentally changed (Underwood 1986). To use an extreme example, if one tests the effects of heat-branded rainbow trout (*Oncorhynchus mykiss*) on Atlantic salmon in small lentic aquaria with no substrate or cover under abnormal photoperiod, and when feeding pelleted food, then the hypothesis being tested will have little relevance to natural conditions in streams, even when properly controlled and replicated.

Additive and substitutive designs

There are two basic questions that can be asked about interspecific competition, leading to two different experimental designs. First, does adding species B have any effect on species A, all other things equal? Second, if so, does adding species B have any more (or less) effect than adding the same number of species A (Connell 1975, 1983). The first question leads to an additive design that tests the *existence* of interspecific competition, the second to a substitutive design that measures its *strength* relative to intraspecific competition. Both have advantages and disadvantages (Begon et al. 1996) and situations to which each applies best. A design that combines both is ideal, but may be logistically impossible. Each design is treated seriatim.

Additive designs are most useful to address the effects of nonnative species, and competitors that differ markedly in size or ecology. Treatments are typically constructed by adding an equal density of the competitor, compared to controls with ambient density of the target species (Table 1). The advantage of this design is that it holds "all other things equal" (e.g., intraspecific competition; Werner and Hall 1977) except for adding the competitor, a hallmark of logical experimentation (Underwood 1986, 1997; Snaydon 1991). However, it also confounds the effect of interspecific competition with that of doubling total density (Maiorana 1977; Law and Watkinson 1987, 1989). Thus, if performance of species A declines when species B is added, one cannot de-

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Table 1. Two different designs for testing relative strengths of interspecific versus intraspecific competition. The additive design is favored by Underwood (1986) and Dunson and Travis (1991).

	Experimental treatment		
Characteristic	1	2	3
Additive design			
Number of species A	5	5	
Number of species B		5	5
Substitutive design			
Number of species A	10	5	
Number of species B		5	10

termine whether species B has any greater effect than adding an equal number of species A, without further experiments (Table 2). Despite this, because it models the process of species invasion it is the most logical design to answer whether nonnative species affect native ones, or whether removing a nonnative competitor will allow a reduced population of a native species to rebound. If not, then some factor other than interspecific competition is affecting the native species. This design is also the most useful when competitors are of different sizes or have different ecology so that total density has little meaning (Snaydon 1991). For example, Beall et al. (1989) tested the effect of yearling coho salmon (*Oncorhynchus kisutch*) on emerging Atlantic salmon using an additive design, which was appropriate because the two are very different sizes. In such experiments it would be logical to use either natural densities or equal biomasses of each species.

Substitutive designs, in contrast, are most useful for assessing the relative effect of one native species on another, where both are similar in ecology and already known to compete. Because animals are expected to be ecologically more similar to their own species than another, one would expect conspecifics to be stronger competitors than heterospecifics. This led Connell (1975, 1983) to propose that the strength of interspecific competition can only be understood in comparison to intraspecific competition. By holding total density constant (Table 1) the substitutive design can be used to determine relative strengths of interspecific versus intraspecific competition, whereas the additive design confounds the effect of the added competitor with increased density and is unable to distinguish two of the three possibilities (Table 2; Dunson and Travis 1991). Substitutive designs work equally well, and additive designs suffer the same deficiency, in cases where a species responds to a superior competitor that dominates a preferred habitat like pools by shifting to use a less favorable habitat such as riffles (i.e., via a niche shift or interactive segregation). However, others argue that the substitutive design is invalid because it changes the two factors simultaneously (Underwood 1986; Snaydon 1991).

In practice, for coevolved species such as Atlantic salmon and brown trout (*Salmo trutta*) which are similar in ecology and already known to compete behaviorally for food and space (e.g., Kalleberg 1958) using the additive design to test the null hypothesis that brown trout have no effect on Atlantic salmon (not even an effect equal to other salmon) may be of little interest (see Dunson and Travis 1991; Gilliam et al. 1993 for similar examples). Instead, managers may want to use the substitutive design to measure the effects of stocking age-0 brown trout on age-0 Atlantic salmon (interspecific competition) relative to stocking the same number of Atlantic salmon (intraspecific competition). Similarly, this design could be used to ask whether resident brown trout survival would be higher if rainbow trout were stocked versus more brown trout, in waters where one or both are not native. In both cases, the question of interest is best addressed with the substitutive design that contrasts interspecific competition versus added intraspecific competition.

An ideal approach would combine both additive and substitutive designs to test both the existence and relative strength of interspecific competition. This requires a minimum of five treatments to allow separating reciprocal intraspecific versus interspecific effects for two species (see Underwood 1986, 1997; Fausch 1988; Dunson and Travis 1991). Logistical constraints inherent in working with large mobile organisms like stream fish often require minimizing treatments to permit adequate replication (Fausch 1988), so many investigators have reduced designs to the three treatments shown in Table 1, or the minimum of two needed to measure the effect of a competitor on one target species (e.g., 10 species A versus 5 A plus 5 B). In what follows I refer to designs with the three treatments as "full additive" or "full substitutive," and those with two treatments as "minimal additive" or "minimal substitutive" designs.

The two designs described above have long been used by plant population biologists (deWit 1960; Harper 1977; Firbank and Watkinson 1985). Because plant densities and mixtures are more easily manipulated under controlled conditions, a preferred design involves measuring performance under a wide range of frequencies and densities of both species and fitting a response surface (Law and Watkinson 1989; Firbank and Watkinson 1990). However, such large experiments would be impossible for most vertebrates and are not considered further.

Two other experimental design issues are also important. First, the relative intensity and magnitude of intraspecific and interspecific competition depend on the starting densities used. Ideally, experiments would be conducted at carrying capacity for both species. Alternatively, experiments can be designed based on the range or mean of natural densities measured in the field at sites to which the inferences will be applied, or run at a series of densities to assess the density dependence of competition. For an experimental channel, carrying capacity can be operationally defined by stocking fish at high density and removing individuals that emigrate through traps more than twice (cf. Fausch 1984; Fausch and White 1986). Second, body size often determines the outcome of competition among stream salmonids, which compete for territories in relatively homogeneous habitat such as riffles or glides (e.g., Kalleberg 1958) or set up size-structured dominance hierarchies in pools (e.g., Fausch 1984). Therefore, experiments using the designs described above should be run with fish of equal sizes, or the natural range of sizes, depending on the hypothesis being tested (cf. Fausch and White 1981, 1986; MacCrimmon et al. 1983). Finally, testing interspecific competition within size-structured hierarchies requires an individual-based theory in-

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Table 2. Per capita performance of species A (e.g., growth) in treatment 2 (interspecific competition; see Table 1) when compared to treatment 1 (intraspecific competition for species A), for two experimental designs and three scenarios of relative strengths of interspecific versus intraspecific competition.

Design	Interspecific >> intraspecific	Interspecific = intraspecific	Intraspecific >> interspecific
Additive	Decreased growth (confounded[a])	Decreased growth (confounded[a])	No growth difference
Substitutive	Decreased growth (unconfounded)	No growth difference	Increased growth (unconfounded)

[a]Effect is confounded because it could be due either to adding the competitor, or increasing the total density, or both.

corporating behavioral interactions, which is beyond the scope of this paper. Readers are referred to Fausch (1984), Parker and Sutherland (1986), and Milinski and Parker (1991) for possible approaches.

Practical constraints

What of the "real world" of testing interspecific competition, where logistic, economic, and ethical considerations all play strong roles in determining which research is actually conducted? Many researchers and managers must settle for conducting research that may not conform to the ideal standards above. One such line of evidence is comparative analysis of many field sites where a competitor is present versus absent. Although very useful for generating testable hypotheses, the effect of the competitor is confounded with differences in environmental factors among locations, a problem that may be addressed only with a large sample of sites and analysis of covariates (e.g., temperature). Even so, at these large scales it is difficult to rule out alternative hypotheses for the patterns (Connor and Bowers 1987; Wiens 1989), such as differences in abiotic (e.g., altitude, gradient) or other biotic factors (e.g., predation, disease), or interactions among them. Fausch (1989) and Fausch et al. (1994) present these kinds of analyses.

Because setting up enclosures and manipulating densities may itself introduce unwanted effects on fish, one of the simplest ways to conduct a competition experiment is by removing the competitor and comparing the response of the target species before versus after (e.g., Fausch and White 1981) or to that in an unmanipulated control reach. This is, in effect, a minimal additive design (Table 1) and is particularly useful for determining whether a nonnative invader has effects at least as strong as conspecifics (Table 2).

Finally, it is important to realize that one experiment does not a complete understanding make. The ideal circumstances are to conduct multiple experiments in both laboratory and field, and combine these with observational field data at various scales. Thus, whereas tightly controlled and replicated experiments can be used to test focused hypotheses about the mechanisms of competition, broad field surveys will be important for placing the results into an appropriate context for resource managers.

Coevolved competitors

Atlantic salmon coevolved with brook trout (*Salvelinus fontinalis*) in North America and brown trout in Europe, and occur in sympatry with both as juveniles in streams. They also coevolved with other salmonids (e.g., Arctic charr, *Salvelinus alpinus*) and nonsalmonids (e.g., *Rhinichthys atratulus, Cottus gobio*), but only one experiment has been conducted on interactions with any of these (Symons 1976). Here I use the framework of scale and experimental designs laid out above to review the experiments that have been done and, ultimately, to address three questions. First, which studies have used controlled and replicated experiments with designs appropriate for the question of interest to yield valid inferences at any scale? Second, what information do we have at larger scales along the four axes, such as for populations in local patches over annual increments? Third, how might the answers change across scales?

Brook trout

Brook trout alevins emerge from gravel redds before Atlantic salmon in spring and are therefore larger (Randall 1982) and presumably dominant in their preferred habitat. Observational evidence indicates that age-0 brook trout use positions in pools whereas age-0 Atlantic salmon occupy riffles (Gibson 1993; Rodríguez 1995). However, when allopatric each species may use the opposite habitat (MacCrimmon et al. 1983) suggesting that in sympatry niche shifts due to interspecific competition, also known as interactive segregation (Nilsson 1967), may be occurring. If so, interspecific competition by either species may have negative effects on growth or survival (and hence biomass or density) of the other that are stronger than intraspecific competition.

Few controlled experiments have been done that can adequately answer these questions for brook trout and Atlantic salmon, primarily because most were unreplicated and in several additive designs were used that prevent determining the relative strength of interspecific competition (Table 3). For example, Gibson et al. (1993) reported on a long-term, large-scale manipulative experiment in three southeast Newfoundland streams. Microhabitat selection and salmonid biomass in individual habitat units (i.e., riffles, flats, pools) were measured 2 years before and 5 years during which spawning Atlantic salmon were placed above a migration barrier into a stream with only brook trout. Another stream with brook trout alone was used as a control, and a third stream had brook trout and wild salmon. After stocking, total salmonid biomass in three riffles of the stream where salmon were stocked was about half that in two riffles of the stream with brook trout alone, but because there were no replicate streams this difference could have been due to factors unique to each. Moreover, the design was confounded because pretreatment densities in the specific habitat types being compared varied 2 to 5 times among different streams. Similarly, not all data for all habitat types sampled, nor all streams, were provided, preventing further analysis. The

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Table 3. Design and main results of controlled experiments testing competition between Atlantic salmon and coevolved competitors. Spatial scale is of the entire experimental unit manipulated, even though responses may have been measured at a smaller scale. Full and minimal additive (A) and substitutive (S) designs are described in the text and Table 1. For replicated experiments only, the relative strengths of intraspecific (intra) versus interspecific competition (inter) are shown as the outcome.

	Scale							
Reference	Space (m^2)	Time (d)	Biological response	Biological organization	Experimental unit	Replication	Design	Outcome
Brook trout								
Dickson and MacCrimmon (1982)	0.90	14	Behavior, growth	Individual	Tank	7–11	Full S	Intra = inter[a] for both responses
Gibson and Dickson (1984)	1462–4075[b]	64–79[b]	Growth, biomass	Individual, "population"[c]	Reach	1–2	Minimal A[d] (add trout)	Unreplicated
Gibson and Power (1975)	7.5	>1[b]	Behavior	Individual	Tank	1	S[e]	Unreplicated
Gibson et al. (1993)	ca. 38 000[b]	ca. 2190	Behavior, biomass	Individual, "population"	Stream	1–2	Minimal A[f] (add salmon)	Unreplicated
MacCrimmon et al. (1983)	0.90, 5.25	14, 29	Behavior, growth	Individual	Tank, enclosure	7–11, 2–3	Full S	Asymmetry for behavior, intra = inter for growth[g]
Brown trout								
Kennedy and Strange (1980)	ca. 1980, 8880	ca. 730	Growth, density, survival	Individual, "population"	Stream	2	Minimal A[h] (add salmon)	Inter ≥ intra for both responses
Kennedy and Strange (1986*a*,*b*)	ca. 2960[i]	ca. 730	Behavior, growth, survival	Individual, "population"	Reach	1	Minimal S (add trout)	Unreplicated
Non-salmonids								
Symons (1976)	26.6	21	Behavior, growth	Individual	Tank	2–3	Full A[j]	Intra > inter for salmon, inter > intra for others

[a]Results suggested intraspecific > interspecific for growth of both salmon and brook trout, but low power may have prevented detecting it.
[b]Data to calculate area of sites or duration of experiments were not given for many or all cases.
[c]Refers simply to all fish present in each reach studied, not to a defined interbreeding population.
[d]Densities not measured for most treatments, so can't separate effects of changes in density from added/removed competitors.
[e]Minimal substitutive (shallow tank) and full substitutive (deep tank) experiments, but densities were not equal among treatments.
[f]Pre-treatment densities varied 2 to 5 times among habitat types between treatments, and post-treatment densities were reported only for some habitats.
[g]Brook trout were 13% longer in enclosures, equal size in tanks. Low power for enclosure experiments masked large differences in growth. Experiments in tanks were the same ones described in Dickson and MacCrimmon (1982).
[h]Total density after salmon were stocked was 2.5–3.8 times higher than for brown trout alone in the two streams over 2 years.
[i]Based on mean width from Kennedy and Strange (1980). Exact dimensions not reported.
[j]Only ranges of densities of nonsalmonids were reported, but were about twice that of salmon.

lack of replication and incomplete data reporting are unfortunate given that these experiments addressed changes in brook trout biomass in whole streams over 7 years. This is the largest temporal and spatial scale of any experiment reviewed (Fig. 1) and just the scale at which managers need answers.

An interesting set of experiments by Dickson and MacCrimmon (1982) and MacCrimmon et al. (1983) can be used to assess whether answers about interspecific competition change across a small range of scales. They studied microhabitat use, agonistic behavior, and growth of brook trout and both wild and hatchery Atlantic salmon in controlled environments at two different spatial and temporal scales, in compartments in an outdoor stream tank (<1 m^2, 14 d) and enclosures in a nearby stream (ca. 5 m^2, 29 d). They measured changes in agonistic behavior (stream tank only) and microhabitat use and growth for both species in allopatry and sympatry, using the full substitutive design (Table 1). The two experiments differed in that species were of equal size in the stream tank, but brook trout were 13% larger in the stream enclosures, which is the natural size differential due to their earlier emergence. Comparisons of wild salmon and brook trout showed that growth was similar and not significantly different among sympatry and each species in allopatry in the stream tank, indicating that interspecific and intraspecific competition were about equal and symmetric

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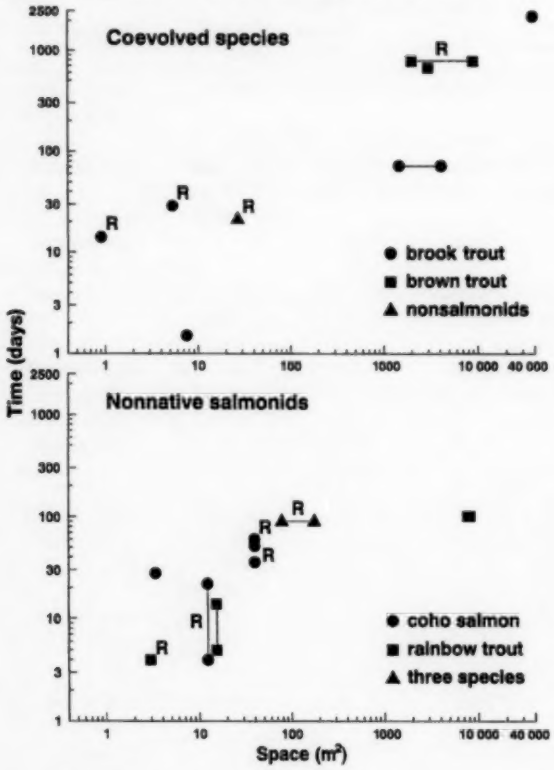
Fig. 1. Spatial and temporal scales of experiments testing interspecific competition between Atlantic salmon and coevolved fishes (top) and nonnative salmonids (bottom). Lines show ranges of scale for different sites in single experiments, and replicated experiments are marked (R). Some points were offset slightly to enhance clarity. Data are in Tables 3 and 4.



when fish were the same size. In contrast, brook trout greatly suppressed growth of Atlantic salmon in sympatry compared to allopatry in the stream enclosures. Unfortunately, this difference was not significant due to few replicates that caused low statistical power. Brook trout also apparently displaced the smaller Atlantic salmon from beneath cover into open positions in the enclosures, whereas in the stream tank both won similar numbers of interspecific bouts. Overall, although the differences in scales were not large and some inferences were hampered by low statistical power, it is reassuring that results from both experiments supported the hypothesis that brook trout dominance increases as they become larger than salmon.

Brown trout

Like brook trout, brown trout alevins emerge before Atlantic salmon and are larger throughout their first year of life in European streams (Egglishaw and Shackley 1973, 1977, 1985). Observational studies on sympatric populations indicated that age-0 salmon used shallow swift riffles during summer and fall, whereas age-0 brown trout used the shallow margins of runs and pools where velocity was lower (Jones 1975; Egglishaw and Shackley 1982; Kennedy and Strange 1982; Heggenes et al. 1995). Age-1 salmon parr used a variety of habitats with different depths, whereas age-1 and older brown trout were found primarily in deeper runs and pools. Early reports suggested that trout dominated salmon, even at the same size (Kalleberg 1958), and that age-0 salmon shifted to use different habitats in allopatry than sympatry with trout (Lindroth 1956; Heggenes 1990). Salmon are thought to be better adapted for riffles than trout due to their larger pectoral fins (Jones 1975; Arnold et al. 1991) and lower buoyancy (Sosiak 1982).

These data, as well as correlative evidence on changes in density resulting from different combinations of sympatry and allopatry (Mills 1969; Gee et al. 1978), led investigators to suspect that, as for brook trout, interspecific competition by brown trout might be important in affecting Atlantic salmon habitat use and, ultimately, growth and survival. For example, Egglishaw and Shackley (1973) stocked advanced salmon ova in a Scottish trout stream so that the fry produced were 12 mm (fork length) longer than the native brown trout by the end of the growing season. They reported high survival rates of salmon compared to nearby streams. Similarly, competition from Atlantic salmon might affect brown trout. These are important problems because managers are interested in maximizing Atlantic salmon production when fry are stocked in streams with brown trout (Mills 1969) and in other cases are interested in maximizing brown trout fry survival in streams stocked with salmon (Saltveit 1993). To resolve both issues would require experiments that incorporate substitutive designs.

Unfortunately, as for brook trout, few experiments provide sufficient evidence to address relative strengths of interspecific and intraspecific competition between brown trout and Atlantic salmon (Table 3). Kennedy and Strange (1980) stocked salmon ova during March each of 2 years in two streams tributary to a reservoir in northern Ireland. Growth and density of trout and salmon were measured and compared to the year before stocking when only trout were present. They reported significant reductions in mean length of age-0 trout and salmon after the second year of stocking in one stream. They also found marked declines in density of age-0 trout, and survival of age-0 salmon, but only during the second year of salmon stocking in both streams. Because age-1 salmon parr were not present until the second year, they attributed the declines in density and survival to competition from the salmon parr rather than fry. However, while the study was minimally replicated (n = 2 streams) and controlled in time (via pretreatment data), it cannot be used to assess whether interspecific competition from salmon was any greater than intraspecific competition from trout. This is because total salmonid density was increased 2.5–3.8 times, among the replicates and years, by stocking the salmon, thereby creating an additive design (see Tables 1 and 2). Thus, similar effects on growth and survival of trout fry might have resulted from heightened intraspecific competition, if trout density alone had been increased this much.

Kennedy and Strange (1986*a*, *b*) conducted an unreplicated experiment to measure the effect of brown trout on Atlantic salmon behavior, growth, and survival. They constructed a weir dividing one of the streams described above in half and removed brown trout from the upstream half using rotenone. Salmon ova were again stocked for 2 years and the resulting assemblages sampled the fall and

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spring after each stocking. Fortunately, total salmonid densities were similar between sections over the four samples, their means varying by only 4%, resulting in a minimal substitutive design (Table 1).

The experiment demonstrated that interspecific interactions by all ages of brown trout on Atlantic salmon were stronger than intraspecific interactions among salmon, although without replication one cannot determine how much was due to differences between the sections. Growth and density of age-0 salmon were lower in the reach with brown trout than without in both years, even though the second year age-1 salmon parr were also present and had an additional effect (Kennedy and Strange 1986*b*). During the second year of the experiment, density of the age-1 salmon parr remaining was also higher in allopatry than sympatry, suggesting that brown trout also reduced parr density. Moreover, this effect may have been underestimated due to apparent downstream dispersal of salmon from the allopatric to sympatric section over winter, and possible increased growth in allopatry that may have increased the number of parr smolting as age-1+. Changes in habitat use were also evident, with age-0 salmon selecting deeper habitat when alone or with age-1 salmon parr than in sympatry with all age classes of brown trout (Kennedy and Strange 1986*a*). In contrast, age-1 salmon used deep habitat with or without trout, as did all age classes of trout including age-0.

Although the experiment suggested that interspecific competition from brown trout changed behavior of juvenile Atlantic salmon and reduced their growth and density beyond that due to intraspecific competition, an alternative hypothesis is that salmon fry were restricted to shallow habitats by predation risk from older brown trout in deeper habitats (Kennedy and Strange 1986*a*; Bardonnet and Heland 1994). Stomach sampling indicated that some predation occurs (Kennedy and Strange 1986*a*), especially just after fry emergence (Kennedy and Strange 1980), but density-dependent interspecific and intraspecific competition probably play a larger role. Further research would be needed to assess the relative strengths of predation and competition. Although the experiment by Kennedy and Strange (1986*a*,*b*) did not fully test cause and effect because it was unreplicated and could not rule out alternative hypotheses such as predation, the results were biologically significant and can be used to plan further replicated experiments.

LeCren (1965, 1973) described experiments where different proportions of Atlantic salmon and brown trout eggs were stocked in enclosed sections of a small Scottish stream. Although no details of methods or results were given, he reported that mortality of the resulting trout fry was proportional to trout density alone, whereas mortality of salmon fry depended on density of both species. He inferred from this that trout dominated salmon under these conditions. Further analysis of these data, if extant, might prove fruitful.

Nonsalmonids

Symons (1976) conducted an experiment in a laboratory stream using the full additive design to assess interspecific competition between Atlantic salmon and four nonsalmonids frequently found sympatric with them in eastern North American streams (Table 3), blacknose dace (*Rhinichthys atratulus*), common shiner (*Luxilus cornutus*), creek chub (*Semotilus atromaculatus*), and white sucker (*Catostomus commersoni*). He found that salmon preferred boulder and open stream habitats and easily displaced nonsalmonids from them at fast and slow velocities, whereas without salmon the nonsalmonids shifted to use these habitats. Growth of dace and suckers was depressed when sympatric with salmon in fast velocity trials relative to allopatry. Overall, there was a clear pattern of stronger intraspecific than interspecific competition for salmon, using the additive design appropriate for competitors of different size and ecology (see above). In contrast, for the three nonsalmonids interspecific competition was at least as strong as intraspecific and may have been stronger, given the strong exodus from habitats used by salmon when all species were sympatric.

Nonnative species

Nonnative species of salmonids, particularly coho salmon (Harache 1992) and rainbow trout (Hearn and Kynard 1986), have often been introduced into the native range of Atlantic salmon in both North America and Europe. Concern has been raised repeatedly about the potential for negative effects should these introduced species become established (Gibson 1981; Fausch 1988; Mills 1989). What experimental evidence can be brought to bear on this issue?

Coho salmon

Beall et al. (1989) conducted four experiments in indoor and outdoor artificial streams to test the effects of three life stages of coho salmon (emerging fry, older fry, and yearlings), and Atlantic salmon yearlings, on newly emerged Atlantic salmon fry behavior, growth, and survival (Table 4). Two experiments in the outdoor channels were generally well designed and yielded clear results. In one, older coho fry had strong interspecific effects on survival and growth of emerging Atlantic salmon, probably because coho had a large size advantage (ca. 14 mm). Based on their data, a 7–11-mm size advantage might be expected if coho emerged naturally (Beall et al. 1989). In the other experiment, yearlings of both species increased emigration and decreased growth of Atlantic salmon fry, with stronger effects from yearling Atlantic salmon than coho, but neither species preyed on fry. Both experiments used additive designs appropriate for questions about competition from invading species, and different age classes that vary in size, but the total biomasses of the two species were probably not equal in either.

In contrast to older juvenile and yearling coho salmon, experiments with emerging fry, conducted both in homogeneous laboratory troughs (3.4 m^2) and outdoor riffle-pool channels (ca. 40 m^2), gave conflicting results. While residency of emerging Atlantic salmon was strongly reduced by emerging coho in the laboratory stream, intraspecific competitors had the stronger effect on both species in the outdoor channel, probably because the heterogeneous habitat in the latter allowed normal habitat segregation of Atlantic salmon into riffles and coho into pools. The difference could not be explained by initial density, which was high but similar in the two experiments. Neither experiment on emerging

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Table 4. Design and main results of controlled experiments testing competition between Atlantic salmon (AS) and nonnative competitors (coho salmon [CO], rainbow trout [RT], and both with brown trout [BT]). Full and minimal additive (A) and substitutive (S) designs are described in the text and Table 1. For replicated experiments only, relative strengths of intraspecific (intra) versus interspecific competition (inter) are shown as the outcome.

		Scale							
Reference	Life stage	Space (m^2)	Time (d)	Biological response	Biological organization	Experimental unit	Replication	Design	Outcome
Coho salmon									
Beall et al. (1989)	1. Emerging fry	40.4[a]	52[b]	Behavior, growth, survival	Individual, "population"[c]	Reach	1	Full S	Unreplicated
	2. Emerging fry	3.4	28	Behavior	Individual	Tank	1	Full S	Unreplicated
	3. Emerging AS with older CO fry	40.4[a]	61	Behavior, growth, survival	Individual, "population"	Reach	3	Minimal A (add CO)	Inter >> intra for AS for all responses
	4. Emerging AS with CO or AS yearlings	40.4[a]	36	Behavior, growth, survival	Individual, "population"	Reach	2	Full A	Inter > intra for fry with either spp.
Gibson (1981)	Older juveniles	14.3	4–22	Behavior, growth	Individual	Tank	2–3	Full A	—[d]
Rainbow trout									
Gibson (1981)	Older juveniles	14.3	5–14	Behavior, growth	Individual	Tank	1–2	Full A[e]	—[d]
Hearn and Kynard (1986)	1. Age-0 and age-1 (lab stream)	3.0	4	Behavior	Individual	Tank	3–9	Full A[f]	Intra > inter for age-0 AS, inter ≥ intra for age-1 AS
	2. Age-0 (natural stream)	ca. 7945, 8338	101	Behavior	Individual	Reach	1	Minimal A (add AS)	Unreplicated
Combination of nonnative salmonids									
Jones and Stanfield (1993)	Age-0 CO, ages-0 and -1 BT, age-1 RT	80–180	ca. 90	Growth, survival	Individual, "population"	Reach	4	Minimal A (add nonnative spp.)	Inter ≥ intra for AS

[a]An estimate from the information given, because lengths of outdoor channel reaches were not reported.
[b]Calculated from beginning of fry emergence to end of experiment.
[c]Refers simply to all fish present in each reach studied, not to a defined interbreeding population.
[d]The same fish were used repeatedly in various replicates of the three different treatments (see Table 1), so results were not independent.
[e]Densities for one species were not equal in sympatry and allopatry.
[f]For age-0 Atlantic salmon, density was unequal in allopatry, and results of a full substitutive design were not reported.

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fry was replicated, however, so no strong inferences can be made.

Rainbow trout

Hearn and Kynard (1986) studied interactions between juvenile Atlantic salmon and rainbow trout in a laboratory stream and two reaches of a natural Vermont stream bounded by weirs (Table 4). In the laboratory stream age-0 Atlantic salmon used riffles, runs, and pools equally when alone and when age-0 rainbow trout were added (in an additive design), suggesting that intraspecific competition among salmon was greater than interspecific competition with trout (Table 2). In contrast, age-1 salmon showed a significant shift toward riffle habitat when age-1 trout were added, indicating that the trout had a competitive effect. Both age-0 and age-1 trout preferred pools with or without salmon, indicating that for them intraspecific competition was stronger than interspecific. For both ages and species, agonistic behavior was more frequent between conspecifics than heterospecifics (except for age-0 salmon). However, rainbow trout initiated 3 to 4 times more aggressive behavior than Atlantic salmon at each age and attacked age-1 salmon twice as much as vice versa. This greater aggression by trout yearlings may help explain their apparent dominance over salmon in pools.

In the field experiment, more than twice as many age-0 rainbow trout emigrated from an allopatric control section than one stocked with Atlantic salmon (Hearn and Kynard 1986), even though total salmonid density was 20% less in the control. Although the experiment was unreplicated, it suggests that intraspecific competition among wild rainbow trout is stronger than interspecific competition with stocked salmon.

Combinations of nonnative species

Reestablishment of Atlantic salmon to Lake Ontario, to which they were native, will require stocking them in tributaries that support nonnative salmonids, including coho salmon, brown trout, and rainbow trout. Jones and Stanfield (1993) conducted a controlled and replicated field experiment in short reaches of one such tributary (Table 4) to test the effects of competition from this suite of species on growth and survival of stocked large Atlantic salmon fry (mean total length 72 mm). Growth was 39% higher and survival 136% higher (both significant; $P < 0.001$), on average, at sites where nonnative salmonids had been removed by electrofishing before the experiment than paired sites with similar habitat where their abundance had been estimated but the fish returned. This additive design was appropriate to address whether competition from nonnative salmonids (or perhaps predation by the older fish) could negatively affect Atlantic salmon stocked for restoration, and also stands as the best example of a controlled and replicated field experiment conducted at appropriate scales along the four axes outlined above. Jones and Stanfield (1993) also concluded that the effect could not be explained by competition from mottled sculpin (*Cottus bairdi*) or age-0 rainbow trout, because these were not effectively removed by electrofishing and so were at similar density in both sympatry and allopatry.

Gibson (1981) also studied interactions between Atlantic salmon and either coho or steelhead in a laboratory stream. However, in many cases the same fish were used repeatedly in different replicates and treatments of the same experiments so results were not independent.

Complex interactions

Despite the difficulty of carrying out experiments to adequately test competition between two species under one set of conditions, more detailed studies will ultimately be needed to fully address the complex set of interacting factors that are likely important in nature. For example, for coevolved competitors the relative strengths of interspecific and intraspecific competition often vary with temperature, habitat, or other factors, so that each species dominates in different parts of the environment (Dunson and Travis 1991), thereby promoting coexistence (McPeek 1990). Dunson and Travis (1991) termed such interactions condition-specific competition (see also Power et al. 1996; Poff 1997 on context-dependent interactions) and described a protocol for testing for them.

Condition-specific competition may also explain why results for the same species change across spatial scales. If larger stream enclosures or reaches incorporate the full range of habitat complexity in which two species evolved, such as riffles and pools, then it is likely that each species will be successful in the portion that includes its realized niche. In contrast, restricting the species to only one habitat or confining them to habitat that is too simple in an artificial channel may allow one species to dominate. This may explain why results differed markedly for emerging Atlantic salmon and coho fry tested at two different spatial scales by Beall et al. (1989). It also suggests that if research is to address managers' questions about competition in natural habitat it will need to be conducted at the largest scale at which adequate control and replication are possible.

Information on condition-specific competition will be most important for predicting how Atlantic salmon populations will respond to altered conditions. These include effects of nonnative species introductions and potential reversals in dominance of coevolved or introduced species when environmental factors such as temperature (e.g., Reeves et al. 1987; DeStaso and Rahel 1994) and flow regime are changed by human agents. For example, nonnative rainbow trout have been unsuccessful at establishing reproducing populations throughout much of Europe where brown trout are native, except in places like eastern Switzerland and Liechtenstein. Here, dikes were built along the upper Rhine River and new channels parallel to the river were created on the former floodplain to drain water from its tributaries. These channels have very stable flow and temperature regimes and are rarely disturbed by flooding. This modification has apparently favored rainbow trout, which now reproduce and reach high densities in a region where streams were once inhabited solely by brown trout (A. Peter, Swiss Federal Institute for Environmental Research, Kastanienbaum, personal communication).

A second class of complex interactions that may ultimately be important are indirect effects through food webs, caused either by nonnative species or the effects of humans. Recent work in New Zealand indicates that introduction of nonnative salmonid predators may affect invertebrate prey

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behavior and ultimately alter the structure and productivity of entire food webs (Flecker and Townsend 1994; McIntosh and Townsend 1994). Nonnative salmonids like rainbow trout or coho salmon might also cause such indirect effects, thereby affecting sympatric Atlantic salmon. Similarly, Wootton et al. (1996) recently proposed that regulating river flow has strong indirect effects on salmonids by releasing a predator-resistant grazing caddisfly (Trichoptera) from scouring floods that kept population numbers down. In regulated rivers these grazing caddisflies depressed algae that reduced production of other grazers on which fish fed. Overall, it is clear that fish ecologists will need even more sophisticated experimental approaches incorporating entire river food webs on which salmonids depend to assess the relative strengths of complex interactions like these.

Conclusions

Overall, there is relatively little evidence from which to judge the effects of interspecific competition on juvenile Atlantic salmon at any scale. More than half the experiments reviewed were unreplicated (9 of 17) and therefore inadequate to test either the existence or relative strength of interspecific competition between juveniles of Atlantic salmon and other fishes (Tables 3 and 4). In contrast, for all but one of the eight replicated experiments, experimental designs were appropriate to address the questions of interest. Thus, for nonnative species, and nonsalmonid competitors of different size or ecology, additive designs were used to test the existence of interspecific competition in all five cases. For coevolved salmonids with similar ecology, substitutive designs were used to test the strength of interspecific competition relative to intraspecific in two of three experiments. A plot of spatial and temporal scales of replicated experiments revealed that at least minimal replication was possible over a broad range of scales (Fig. 1), including a study that spanned 2 years and ca. 9000 m^2 of habitat. However, even some of the smallest scale experiments were unreplicated. The best study incorporated adequate replication and an appropriate design in a field experiment conducted at useful scales to address questions about effects of nonnative salmonids (Jones and Stanfield 1993).

The most urgently needed experiments are indeed those testing effects of nonnative salmonids on growth and survival of juvenile Atlantic salmon at appropriate spatial and temporal scales, using fish of the sizes and age classes found in nature. Of the nonnative salmonids considered to date, juvenile coho salmon may have the strongest effect on age-0 Atlantic salmon due to their innate aggressiveness and inherent size advantage caused by earlier emergence and larger size at emergence (cf. Fausch and White 1986; Beall et al. 1989), although habitat segregation by Atlantic salmon into riffles (Gibson 1993; Heggenes et al. 1995) and coho into pools (Hartman 1965; Bisson et al. 1988) may ameliorate this interaction somewhat. In addition to the experiment of Jones and Stanfield (1993), the work of Beall et al. (1989) is a useful model (provided appropriate experimental designs and replication are used), because they conducted experiments on emerging Atlantic salmon at a relevant scale for this life stage, considered several sizes and ages of coho salmon competitors and predators, and explicitly considered the role of emigration. Movement of stream fishes is an important feature to consider in any experimental design, because it can complicate studies of their population biology (Gowan et al. 1994; Gowan and Fausch 1996*a*, *b*), most often by transferring effects from one experimental reach to another (e.g., Kennedy and Strange 1986*b*).

Finally, it is clear that managers will need this knowledge soon for it to be helpful. Introductions of sport fish, and the large amounts of cage culture now underway throughout the world, will continue to release nonnative fish outside their native ranges and further the chances for new invasions (Townsend 1991; Moyle and Light 1996). For example, Atlantic salmon are now reared in sea cages along the Pacific coasts of North and South America (e.g., McKinnell et al. 1997), while Pacific salmonids have been both introduced and cage-reared in the Atlantic Ocean (Harache 1992). Cage culture of Atlantic salmon in British Columbia has apparently produced substantial numbers of spawning adults migrating up rivers (B. Ward, British Columbia Ministry of Environment, personal communication), while native steelhead populations continue to decline for other reasons, leading to the question of whether the combination of these factors may eventually allow Atlantic salmon to successfully invade. In addition, recent efforts to restore Atlantic salmon to their former range in the face of stocked or naturally reproducing nonnative salmonids (e.g., rivers in Belgium stocked with rainbow trout; streams tributary to Lake Ontario, Jones and Stanfield 1993), pose similar problems for managers attempting to predict the potential for Atlantic salmon to be successfully reintroduced.

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The role of context-specific predation in understanding patterns exhibited by anadromous salmon

Martha E. Mather

Abstract: Predation is frequently studied in aquatic systems that contain salmon. Because these systems are difficult to manipulate and replicate, rigorous across-system comparisons are essential. Herein I review the literature on factors that may influence predation across systems. Specifically, I evaluated how often predation on salmonids was important across prey taxa, life stage, habitat, predator taxa, methodology, and spatial scale. Further, I examined what factors were influential in systems where predation was important. In nine journals from 1959–1996, 45 field studies explicitly tested the importance of direct effects of predation on anadromous salmonid prey. Authors of 36 (80%) studies concluded that predation was important. More studies in which predation was deemed important focused on smolts subjected to fish predation in the transitional river and estuary habitats. Furthermore, field surveys at larger spatial scales were most often used. Finally, most studies reported little information on confounding factors that complicate predation. If we are to learn from these complex systems, we need to collect, analyze, and report similar types of information that are collected across systems and years using rigorous and systematic methods.

Résumé : La prédation est souvent étudiée dans des systèmes aquatiques qui abritent des saumons. Étant donné que ces systèmes sont difficiles à manipuler et à reproduire, il est essentiel de pratiquer des comparaisons rigoureuses entre systèmes. J'examine ici la littérature concernant les facteurs qui peuvent influer sur la prédation dans les systèmes. J'ai évalué plus précisément si la prédation sur les salmonidés était importante par rapport aux taxons proies, au stade de développement, à l'habitat, aux données sur les prédateurs, à la méthodologie et à l'échelle spatiale. J'ai de plus recherché quels facteurs avaient de l'influence dans les systèmes où la prédation était importante. Dans neuf revues, entre 1959 et 1996, 45 études de terrain vérifiaient explicitement l'importance des effets directs de la prédation sur les salmonidés anadromes proies. Les auteurs de 36 (80 %) de ces études concluaient à l'importance de la prédation. La majorité des études dans lesquelles la prédation était jugée importante portaient sur les smolts soumis à la prédation par des poissons dans les habitats transitionnels des cours d'eau et des estuaires. En outre, les relevés à grande échelle spatiale étaient les plus couramment employés. Enfin, la plupart des études donnaient peu d'information sur les facteurs qui compliquent l'étude de la prédation. Si nous voulons tirer une leçon de ces systèmes complexes, nous devons recueillir, analyser et rapporter des types d'information similaires qui sont récoltés dans plusieurs systèmes et sur plusieurs années, à l'aide de méthodes rigoureuses et systématiques.

[Traduit par la Rédaction]

Introduction

Predation is an important force in many aquatic communities (Estes et al. 1978; Bronmark et al. 1992; Garvey et al. 1994). This process can affect prey production (Bronmark et al. 1992; He and Wright 1992), behavior (Cooper et al. 1985; Flecker 1992; Fraser and Gilliam 1992), and community structure (He and Kitchell 1990; Holomuzki and Stevenson 1992; Garvey et al. 1994). Predation is of interest in many systems that contain Atlantic (*Salmo salar*) and Pacific salmon (*Oncorhynchus* spp.) because these fish are the object of intensive conservation, restoration, and management. Thus, to sustain this resource, researchers and managers need to understand when, where, why, and how this process affects potential salmonid prey individuals, populations, and communities.

Predators co-occur with potential prey in many systems but do not always have an adverse impact on potential prey (Allan 1982). Even when predators impact prey, the magnitude of the effect varies across systems and years. Identifying and categorizing circumstances that are correlated with strong or weak predation may help us to both understand and predict the implications of this process. In the general ecological literature, many confounding factors influence the strength of the predator–prey interaction including life stage (Schlosser 1987), habitat (Brown and Moyle 1991; Brown and Brasher 1995), predator–prey sizes (Newman and Waters 1984; Bence and Murdoch 1986; Mather and Stein 1993*a*,*b*), spatial and temporal overlap (Schulze 1996), predator and prey numbers (Bence and Murdoch 1986; Johannes 1993; Paszkowski and Tonn 1994; Dettmers and Stein 1996), predator and prey behavior (Cooper et al. 1985; Flecker 1992; Abrahams 1994), predator and

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M.E. Mather. Massachusetts Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Biological Resources Division, Department of Forestry and Wildlife Management, Holdsworth Natural Resource Center, University of Massachusetts, Amherst, MA 01003, U.S.A.
e-mail: mather@forwild.umass.edu

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prey taxa (Abrahams 1994), community structure (Posey and Hines 1991; Holomuzki and Stevenson 1992), environmental heterogeneity (Crowder and Cooper 1982; Fraser and Cerri 1982; Gilinsky 1984; Diehl 1992), abiotic factors (Meffe 1984; Gliwicz 1986; Hayse and Wissing 1996), and season (Posey and Hines 1991). Testing if any of these factors are consistently related to variation in the importance of predation on salmon, especially Atlantic salmon, can help us conserve and manage this important species. Atlantic salmon present unique opportunities for understanding ecological interactions. For example, this charismatic megafauna captures the public imagination, is of economic interest, and integrates the entire ecosystem both laterally and longitudinally. In addition, Atlantic salmon struggle to persist in the face of human impacts and require the integration of both small- and large-scale investigations. However, difficulties exist in studying this intriguing fish, e.g., its distribution and abundance varies greatly across systems; critical linkages exist between life stages, disciplines, and habitats making isolation of individual components difficult. In addition, these fish move great distances, are not distributed evenly, and are difficult to sample. Although the experimental method has so clearly advanced our knowledge in a variety of systems (Platt 1964), whole-system, large-scale processes involving anadromous salmonids are hard to manipulate, impossible to replicate, and difficult to pair with appropriate controls. However, even in these systems, we can still test hypotheses with a rigorous experimental design using carefully planned, well-executed, across-system comparisons.

Herein, I compare the literature across systems and examine when, where, and why predation on anadromous salmonids is important. For example, under what abiotic or biotic conditions do predators have an effect on salmon prey, and conversely, under what developmental, population, community, and environmental circumstances are anadromous salmonids immune from predator effects? Using extant literature, I first qualitatively synthesized what is known about interactions between predators and anadromous Atlantic and Pacific salmon prey. Second, I evaluated the intensity of predation on Atlantic and Pacific salmon prey by comparing predatory demand to prey production in a variety of systems. Third, I counted publications to quantitatively test the importance of predation overall, across-, and within-salmonid prey taxa, life stage, habitat, and predator taxa. Fourth, I quantified the role of 13 confounding factors that have been shown to influence predation in other systems. Fifth, I tested if the relative importance of predation differed with spatial scale or research methodology. Finally, I identified gaps in our knowledge about predator – salmonid prey interactions and suggest future research directions.

Materials and methods

Databases

To assess what is known about predation on salmonids, I searched "salmon" or "steelhead trout" and "predation" or "predator" in nine journals, i.e., *Canadian Journal of Fisheries and Aquatic Sciences*, *Ecology*, *Ecological Monographs*, *Ecological Applications*, *Environmental Biology of Fishes*, *Fisheries*, *Journal of Fish Biology*, *North American Journal of Fisheries Management*, and *Transactions of the American Fisheries Society*, from 1959 to 1996. As a result of this search, I compiled three databases to evaluate five questions. Below, I review criteria for each database and then outline what information was extracted to address these questions.

What is known — question 1, database 1

To review and synthesize qualitative insights into the predation process, I retained all original research that focused on anadromous salmonid prey (Table 1; database 1). These criteria eliminated reviews as well as papers on salmonid predators, stream-resident trout, and Great Lakes salmonids. From papers in this first database, I extracted insights on 13 factors that could influence the strength of the predator–prey interaction, e.g., predator–prey sizes, spatial and temporal overlap, predator and prey numbers, predator and prey behavior, predator and prey taxa, community structure, morphometric complexity, environmental heterogeneity, abiotic factors, and season. I selected these factors somewhat arbitrarily from existing predator–prey literature and certainly not all critical variables were examined. Some studies described baseline conditions of one or more of these factors. To eliminate these descriptions that did not reveal anything new about the variables, for five factors, i.e., size, predator and prey numbers, and predator and prey taxa, I retained only studies in which multiple conditions were concurrently examined or in which the authors explicitly passed judgment on the importance of the factor. For the remaining eight variables, i.e., spatial and temporal overlap, predator and prey behavior, system morphometry, environmental heterogeneity, community structure, abiotic factors, and season, single treatments were included if authors interpreted their findings in a way that added to our knowledge about the role these factors play in predator–prey interactions. For this first database only, a few papers outside of the nine target journals were included if they added specific new insights.

To answer the first question, size described the length of predator, prey, or both. Numbers refers to the abundance or production of predators or prey. Overlap was based on either explicit surveys or implicit reporting of diet overlap. Behavior included foraging, swimming, and migration patterns when options for movement existed. For example, smolt downstream migration was not considered an explicit examination of behavior but flexibility in timing of migration within the window of vulnerability was. Community structure was defined as an examination of interactions among potential prey or predators. System morphometry included larger scale physical features such as system size, configuration, or channel units including riffles and pools. Environmental heterogeneity reflected the author's judgment about the extent of spatial patchiness including the effect of dams. Abiotic factors included temperature, light, discharge, turbidity, and smaller scale physical structures such as cover, substrate, logjams, and overhangs. For season, the authors classification was followed. This first review and synthesis then helped frame the questions used for the quantitative review undertaken in questions two through five.

Context-specific predation: when, where, how, and why — questions 2–4, database 2

To address the second through fourth questions, i.e., (2) what is the relative intensity of predation; (3) which

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Table 1. Criteria used to define the three databases that address five questions on the context in which predation is important or unimportant.

Criteria	Articles
Database 1	
Salmon or steelhead and predation,	134
Anadromous salmonid prey,	118
Original research,	115
Total: Database 1 (Question 1)	115
Qualitatively, what is known about predator – anadromous salmon interactions?)	
Database 2	
Of above, was predation a primary focus,	74
Was quantitative importance assessed,	70
Field or model,	47
Direct effects,	45
Total: Database 2 (Questions 2–4)	45
How does intensity and importance of predation vary?	
Database 3	
In addition to the above, laboratory and field experiments,	68
Indirect effects,	71
Total: Database 3 (Question 5)	71
Does methodology or scale influence importance?	

salmonid prey taxa, life stages, habitats, predator taxa, and (4) key factors influence predation intensity, I used a narrower database composed of comparable, quantitative, field and modeling studies (Table 1). In this second database, I only retained published studies in which predation was the primary focus, data were quantitatively analyzed, a conclusion about the importance or unimportance of predation was expressed by the authors, and in which direct, lethal effects of predation were the focus (Table 1). Four groups of studies were excluded from this second database. First, I did not retain anecdotal predation studies for which the original research objectives were not related to predation. Also excluded from the second database were studies that did not present quantitative results, e.g., no effects of predators on salmon prey numbers, no numerical data on experimental treatments. Third, I eliminated studies in which the author(s) did not explicitly pass judgment on the importance of predation. Consequently, I retained only those studies in which the author(s) concluded that predation was important or unimportant or where the authors reported a substantial or negligible response to experimental treatments implying importance or unimportance in an experimental design that tested the effects of predators. Finally, only field or modeling studies that examined some aspect of mortality were included. For this analysis, if multiple methods, life stages, or habitats were examined within a single paper, each was treated as a separate study. To use this second database to examine question two, i.e., what is the intensity of predation across systems, demand relative to production was defined as the relationship between number of salmonid prey that predators were predicted to consume and the number of prey in the population.

To address questions 3–5, I used an importance index that was defined as the number of studies in which the author of the study concluded that predation was important divided by the total number of quantitative, predation studies using anadromous salmonid prey, i.e., all studies in database 2, (N = 45). In addition, a complementary "unimportance" index was also calculated. In question three, I focused on four factors which could be clearly and unambiguously classified into discrete categories and for which adequate replication existed, i.e., salmonid prey taxa, life stage, habitat, predator taxa. Prey were classified as either Atlantic or Pacific salmon. Based on the author's classification, life stages were categorized as fry, parr, smolt, post-smolt, or adult; habitats as stream, river, lake, estuary, or ocean; and predator taxa as fish, avian, or mammalian, respectively.

Importance indices based on the second database were also used to address the fourth question, i.e., do confounding factors consistently or predictably influence the predation process? All 13 factors identified for the initial qualitative review were evaluated here. These included predator–prey sizes, spatial and temporal overlap, predator and prey numbers, predator and prey behavior, predator and prey taxa, community structure, morphometric complexity, environmental heterogeneity, abiotic factors, and season. This analysis was an attempt to clarify if certain factors influenced the strength of the predator–prey interaction as well as if any methodological bias might influence the results of this review. Specifically, I asked if certain factors were examined or judged influential more often than others. Then, in an attempt at a qualitative analog of a discriminant function analysis, the pattern of examined and influential factors when predation was important was compared to the pattern observed when predation was not important.

For the fifth question, I used importance indices calculated on studies in a third, intermediate-sized database to examine the effects of research methodology and spatial scale (Table 1). For this database, I also included studies that used all methods and which also examined indirect, nonlethal effects. For example, in this third database, laboratory experiments, field experiments, field surveys, and models were included. However, only two broad classifications of spatial scale could be gleaned from the literature, i.e., (*a*) microhabitat measures such as fish home stone or individual range and (*b*) mesoscales that focused on site, reach, or tributary. For this last analysis, studies using only a single scale or method were compared as none of the studies reviewed examined multiple treatments concurrently. Finally, I identified gaps in our knowledge about predator – salmon prey interactions and suggest future research directions.

Results and discussion

Databases

In the nine journals searched from 1959 to 1996, 134 published studies examined relationships between predators and prey (Table 1). The 115 papers that were retained in the first database qualitatively reviewed and synthesized what is known about predation using original research that focused on anadromous salmon prey (Table 1). Predation was the

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primary focus of only 74 papers. Of these, only the 45 quantitative studies in which the author passed judgment on the importance or unimportance of direct effects of predation in the field were retained to address context-specific predation (Table 1; database 2). Database three, created to test questions about methodology and scale, included an additional 26 papers that examined indirect and direct effects using all methods (N = 71 papers; Table 1).

What is known (Question 1)

Overview

Can key features of interactions between predators and salmonid prey be extracted from the published literature in a way that will help us understand when, where, how, and under what ecological, life history, and environmental circumstances intense predation occurs or is avoided? Below, I review and synthesize such qualitative insights from database 1 to summarize what we know.

Size

Size selectivity of predators feeding on salmonid prey varies (Thompson and Tufts 1967; Parker 1971; Hargreaves and LeBrasseur 1985, 1986; Tabor et al. 1993). Although size does not always influence the vulnerability of salmonid prey (Hvidsten and Lund 1988; Carss et al. 1990), in many systems, smaller salmonids are eaten more often (Parker 1971; Hargreaves and LeBrasseur 1986; Poe et al. 1991; Gregory and Levings 1996). In fact, across an array of studies, piscivorous fish consistently select small-sized prey, a pattern possibly mediated by differential size-based capture success (Juanes 1994). To complicate matters, predators often feed first on the largest prey within the population then the smallest as prey grow into then past the maximum size each predator group can consume (Hargreaves and LeBrasseur 1986). In addition, potential prey often pass through a window of vulnerability framed by one predator only to be vulnerable to predation by the next larger piscivore. Thus, prey size selection must be viewed within the temporal and spatial context of the entire predator–prey community.

Theory predicts an array of outcomes relative to predator–prey size. For example, predators may (*a*) maximize a cost/benefit ratio, (*b*) consume the prey that is behaviorally easiest to capture, or (*c*) eat prey that is unusually large or small relative to the mean. Although size may consistently play an important role in determining salmon vulnerability, explicit tests of what is consumed relative to what is available are needed to clarify predictions. Because many avenues exist by which size can influence predator – salmonid prey interactions, to draw generalizations about the role of this factor, we need system-specific information on relative predator and prey size distributions, predator gape range, overlap, dimensions of alternative prey, and size-structured behavior.

Spatial and temporal overlap

For predation to occur, predators and prey must overlap in time and space (Hvidsten and Mokkelgjerd 1987; Gunnerod et al. 1988; Heggenes and Borgstrom 1988; Hvidsten and Lund 1988; Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Beamish et al. 1992; Tabor et al. 1993; Petersen 1994; Beamish and Neville 1995; Beauchamp et al. 1995; Schulze 1996). For example, by changing within-river migration patterns, striped bass (*Morone saxatilis*) predators in the Connecticut River estuary (Connecticut, U.S.A.) overlap with all anadromous prey across all seasons, light periods, tidal stages, and in-river habitats (Schulze 1996). In other systems, timing of migration is also important (Parker 1971; Larsson 1985).

In systems without migratory predators and prey, relatively little variation exists in large-scale patterns of spatial and temporal overlap, and this confounding factor is not particularly interesting or enlightening. However, in systems with migratory prey, especially if not coevolved, substantial variation in predator–prey overlap can exist between years. Furthermore, the survival consequences of minor changes in time of overlap and migration timing can be substantial for mobile predators and prey, and, consequently, spatial and temporal overlap becomes a potentially important and ecologically interesting factor. In the studies reviewed here where predation was positively identified, overlap was, by definition, observed. However, in other systems where predation was not confirmed, overlap or lack of overlap may or may not have been quantified. Lack of information on these complex and often subtle movement patterns can mislead researchers and managers about the relative importance of this factor, and, thus, we need more information on matches and mismatches across systems and years.

Predator and prey numbers

Predator numbers can affect predation intensity (Fresh and Schroder 1987; Rieman et al. 1991; Beamish et al. 1992; Petersen 1994; Beauchamp 1995; Schulze 1996). Specifically, for a constant number of prey, more predators can have a greater impact, and in many systems, more predators do increase the mortality of salmonid prey (Beauchamp 1995; Schulze 1996). Prey numbers can also affect the outcome of predation in several ways (Wood 1987*a*; Heggenes and Borgstrom 1988; Poe et al. 1991; Tabor et al. 1993; Schulze 1996). First, predators may have a greater impact on small prey populations (Schulze 1996). Second, given a fixed number of predators, extremely high numbers of prey produced by a strong year class or prey aggregations can moderate the impact of predation (Wood 1987*a*; Feltham 1990). Third, more prey may attract higher mortality by attracting aggregates of migratory predators (Larsson 1985; Hvidsten and Lund 1988; Beamish et al. 1992; Beauchamp et al. 1995). For example, predation can be more intense during the peak of salmon migration when prey are most abundant. (Poe et al. 1991; Vigg et al. 1991; Tabor et al. 1993; Beauchamp 1995). Similarly, spiny dogfish, *Squalus acanthus*, may be attracted to aggregations of salmon (Beamish et al. 1992), a wall of cod may congregate at the mouth of the river to intercept salmon (Hvidsten and Mokkelgjerd 1987; Hvidsten and Lund 1988), and burbot numbers can increase quickly in response to salmon releases (Larsson 1985). Conversely, although mergansers aggregate in response to increased numbers of salmonid prey, the percent mortality may decrease with increased prey number resulting in depensatory mortality (Wood 1987*a*). Furthermore, the unpredictability of smolt aggregates may

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make these prey difficult for predators to consistently track (Feltham 1990). Thus, enhancement can elicit a variety of responses from predators that may or may not affect potential prey populations depending on relative rates of predator demand and prey production.

Large variations in numbers beyond changes in year class strength may occur seasonally and annually via movements, and this aggregation can have major consequences because migratory predators, like cruise ships, can have an adverse effect on localized prey resources, especially in a non-coevolved system. Although migratory prey may be able to escape predators, aggregation of migratory prey along a fixed, predictable route also allows predators to intercept prey populations. Thus, relative numbers of predators and prey produced both via reproduction or aggregation, the functional response of predators, and predictability of prey migration, need to be quantified to understand and predict the impact of predators on salmonid prey.

Behavior

Predator and prey behavior, i.e., movement, migration timing, foraging behavior, anti-predator responses, and habitat use modifies how many prey are eaten (Hvidsten and Mokkelgjerd 1987; Hvidsten and Lund 1988; Carss et al. 1990; Beamish et al. 1992; Beauchamp et al. 1995). In some systems, predators behave similarly; for example, striped bass, channel catfish, and white catfish in the lower Connecticut River forage and use the river habitat in the same way (Schulze 1996). However, in other systems, predator taxa differ in foraging behaviors (Vigg et al. 1991). In addition, prey behavior can influence predation risk within systems. For example, the higher activity of male salmon during spawning likely contributes to their increased predation by otters (*Lutra lutra*; Carss et al. 1990). Furthermore, prey behavior related to time of movement and behavior during movement can influence predation intensity (Carss et al. 1990; Petersen and DeAngelis 1992).

Foraging behavior of salmonid prey is also linked to vulnerability to predation (Huntingford et al. 1988*a*,*b*; Martel 1996; Ryer and Olla 1996). In the field, habitat use may (Bugert and Bjornn 1991; Magnhagen 1988) or may not (Bugert et al. 1991) change when predators are present. Condition can further affect vulnerability to predation (Gadomski and Hall-Griswold 1992; Mesa 1994). For example, osmotic stress can result in a concurrent change in behavior, and vulnerability to predation (Jarvi 1989; Handeland et al. 1996) such that the migration from the river to the ocean may result in higher mortality because physiologically stressed fish behave in a way that makes them more vulnerable. Hence behavior affects effectiveness of predators and vulnerability of prey in complex ways which must be examined across a variety of conditions to understand when predation does and does not impact prey populations. Furthermore, the specific impact of behavior varies with taxa, system, and life stage, and consequently, the role of this factor needs to be evaluated on a case-by-case basis.

Taxa

A number of predator species including brown trout (*Salmo trutta*), northern pike (*Esox lucius*), striped bass, Atlantic cod (*Gadus morhua*), saithe (*Gadus virens*), common and redbreasted megansers (*Mergus* spp.), gossander (*Mergus merganser*), gulls (*Larus* spp.), otter, and mink (*Mustela visor*) consume salmonids (Anthony 1994). In many systems, predator taxa differ in their impact (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Tabor et al. 1993; Beauchamp et al. 1995). For example, the behavioral shift and recovery time of chinook fry to a model bird predator was greater than that elicited by a model fish predator (Gregory 1993). Similarly, vulnerability to predation can differ with prey taxa (Hargreaves and LeBrasseur 1985; Heggenes and Borgstrom 1988; Dolloff 1993; Beamish and Neville 1995; Healey and Reinhardt 1995; Schulze 1996; Gregory and Levings 1996). Because, the overall predator impact and prey response is a composite of other ecological characters including size, distribution, habitat use, population parameters, and behavior, findings for one predator or prey may or may not be generalizable to other taxa. A functional classification scheme is needed that would allow us to determine when we can and cannot generalize across taxa.

Community structure

A variety of complex interactions may occur in a real community with multiple predators and prey (Hargreaves and LeBrasseur 1985; Poe et al. 1991; Rieman et al. 1991; Tabor et al. 1993; Schulze 1996). For example, two types of predators may eat the same prey type/size and although predation pressure from these additive predators on the target prey type/size may be very high, a refuge for other prey types and sizes exists. Alternatively, when two predator taxa eat different prey types or sizes, predation pressure on any single prey type/size is reduced, but this complementary predator effect eliminates prey refuges. A third community interaction results when alternative prey buffer the effects of predation on salmon. For example, in the Connecticut River returning blueback herring (*Alosa aestivalis*) adults may overlap with the smolt outmigration in some years; if more herring are eaten, smolt mortality may be reduced (Schulze 1996). Similarly, for Pacific salmon, abundant alternative prey late in the run may reduce predation on sockeye fry (Beauchamp 1995). In a fourth community effect, temporally segregated alternative prey may sustain predator populations throughout the year and increase predation on salmon during migration via apparent competition. Finally, although the relative abundance of specific predator and prey taxa may vary, the overall aggregate predation pressure on prey could remain the same as predators come and go. Thus, reducing the number of one type of predator may not increase the numbers of prey if that predator is simply replaced by another. These community effects have very different implications for salmonid prey, and to categorize their impact we need more information on relative abundance, timing of overlap, and interactions among multiple predators and prey.

System morphometry and environmental heterogeneity

System size, channel/estuary dimensions, and basin configuration, collectively referred to as system morphometry, can also influence predation intensity (Roos 1959; Patten 1962; Heggenes and Borgstrom 1988; Rieman et al. 1991; Vigg et al. 1991; Poe et al. 1991). System size may alter predation by increasing duration of predator–prey overlap, reducing condition via physiological migration costs, or

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altering the distribution of migrating fish. Second, estuary/channel size and shape may alter predation by concentrating or diluting predators and potential prey or by altering the availability of refugia. For example, high predation occurs in small streams (Heggenes and Borgstrom 1988), in rapid water below lake outlets, in tributaries, and in small restricted estuaries (Roos 1959; Patten 1962; Hvidsten and Mokkelgjerd 1987). Predatory mortality appears to be more intense when predators and potential salmonid prey are confined together in a simple, unstructured habitat in which prey are forced to interact with predators or where structural complexity favors predators.

Environmental heterogeneity can also change the outcome of predation (Roos 1959; Wood 1987*a*,*b*; Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Petersen 1994; Beauchamp et al. 1995). For example, for northern squawfish (*Ptychocheilus oregonensis*), walleye (*Stizostedion vitreum*), smallmouth bass (*Micropterus dolomieui*), and channel catfish (*Ictalurus punctatus*), consumption rates varied by reservoir area, month, time of day, and predator size or age (Vigg et al. 1991). Similarly, intensity of predation can vary with longitudinal river position resulting in higher mortality within the river compared to the estuary or ocean (Wood 1987*a*; Gunnerod et al. 1988; Ward and Slaney 1990).

Human impacts can increase environmental heterogeneity. Environmental heterogeneity created by dams (Rieman et al. 1991) can slow passage, increase residualism, change the riverine habitat, concentrate predators and potential prey, and create stress that can increase vulnerability to predation, which together result in high mortality immediately below the dam (Geen 1975; Rieman et al. 1991). Thus, heterogeneity created by a disturbance that favors predators exacerbates predation. However, different parts of the same river system can be quite different. For example, squawfish are less important and smallmouth bass more important away from dams (Tabor et al. 1993). In general, examining predation below dams and immediately after hatchery releases may make any estimate of predation unrepresentatively high (Buchanan et al. 1981). Hence the quality, quantity, and spatial arrangement of habitats used by salmonid prey and their potential predators needs to be compared within and across systems to understand the importance of this interaction.

Abiotic factors

Abiotic factors such as temperature, discharge, and water level are also influential. For example, consumption rates of all predators on Pacific salmon smolts were highest in July when temperatures were highest (Vigg et al. 1991). Furthermore, discharge can influence the severity of predation either by intensifying predation at low flows or by altering the habitat at high flows (Patten 1962; Hvidsten and Mokkelgjerd 1987; Heggenes and Borgstrom 1988). Light can affect the relative severity of predation depending on the vision of both predator and prey (Sylvester 1973; Ginetz and Larkin 1976; Patten 1971; Gadomski and Hall-Griswold 1992; Petersen and Gadomski 1994). Other factors that affect vision are also important. For example, chinook fry move from shallow to deep water when predators are present. But turbidity can alter this habitat shift suggesting that in some systems this factor may reduce the susceptibility of prey to predation (Gregory 1993). Although, turbidity does not always directly influence vulnerability to predation (Gregory and Levings 1996). Finally, higher predation also may occur when instream structures that act as refuges are limited (Patten 1962). Thus, abiotic conditions favor heavy predation when they optimize performance of predators over potential prey.

Summary

Predation has a greater effect when (*a*) prey are a size that predators can easily consume, (*b*) predator and prey overlap in time and space, (*c*) predator numbers are large relative to prey numbers, (*d*) predators and prey are aggregated in the same place at the same time, (*e*) no alternative prey is present, and (*f*) preference for the target prey is strong. Predation appears to be most intense when system morphometry, environmental heterogeneity, and abiotic conditions favor predators over prey. Efficient predators and vulnerable prey embody attributes of size, behavior, and habitat use, described above, that make predators efficient and prey susceptible. Seasonality affects predation by altering all of these factors. To build a conceptual framework that describes conditions under which each factor is influential in predator–prey interactions, we need to document variation in these and other factors across years and systems and relate this variability to the strength of predation.

Context-specific predation: when, where, how, and why

Intensity of predation

In some systems predation can be quite substantial. In 12 of 45 studies reviewed, authors estimated the percent of prey population consumed by predators (Table 2). Nine of these 12 estimates of demand relative to production involved fish predators, three examined bird predators. Seven studies focused on Pacific salmon and five on Atlantic salmon. Overall, these 12 consumption estimates ranged from 0.7 to 100% with a mean of 28% of all prey production consumed by predators (Table 2).

Overall importance and prey taxa

For Atlantic salmon, authors of 11 of 14 (79%) quantitative field studies concluded that predation was important in their study systems compared to only 3 (21%) authors that determined that this process was unimportant (Fig. 1). Similar trends existed for other salmonids; specifically, 25 (81%) and 36 (80%) of authors working with Pacific salmon and combined salmonids, respectively, concluded that predation was important (Fig. 1). Because Atlantic and Pacific salmon responses to predation were comparable, we can generalize, to some degree, across taxa. Thus, based on existing studies published in peer-reviewed journals, predation on salmon is important in many systems. However, the strength and consequent implications of the process for salmonid individuals, populations, and communities requires further examination.

Life stage

Data were available to compare the importance of predation for 14 of 15 possible prey taxa-life stage combinations (i.e., three taxa: Atlantic salmon, Fig. 2A, 2D; Pacific salmon, Fig. 2B, 2E; all salmon combined, Fig. 2C, 2F; five life stages per panel: fry, parr, smolt, post-smolt, adult; data not available for Atlantic salmon fry). From 45 field studies

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Table 2. Estimated predator demand relative to prey production for studies examining predation on salmonid prey. ATS is Atlantic salmon; PS is Pacific salmon.

Authors	Predator	Prey	Demand/Production (%)
Beamish and Neville (1995)	Fish	PS	2–65
Beauchamp (1995)	Fish	PS	15
Beauchamp et al. (1995)	Fish	PS	0.7–17.4
Feltham (1995)	Bird	ATS	3–16
Hvidsten and Mokkelgjerd (1987)	Fish	ATS	24.8
Hvidsten and Lund (1988)	Fish	ATS	20
Larsson (1985)	Fish	ATS	50
Rieman et al. (1991)	Fish	PS	14
Ruggerone (1986)	Bird	PS	2
Ruggerone and Rogers (1992)	Fish	PS	59
Schulze (1996)	Fish	ATS	10–100
Wood (1987*b*)	Bird	PS	24–65

Fig. 1. Number of studies published in nine journals between 1959–1996 in which authors judged predation to be important or not important for Atlantic salmon, Pacific salmon, and both salmonids combined. Numbers over the bars represent the total number of studies in which predation was important or not important for each of the three taxa. Whether predation was considered to be important or not important in each study was based on the author's classification.

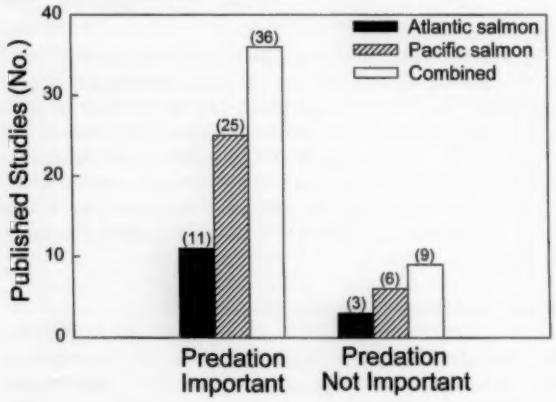
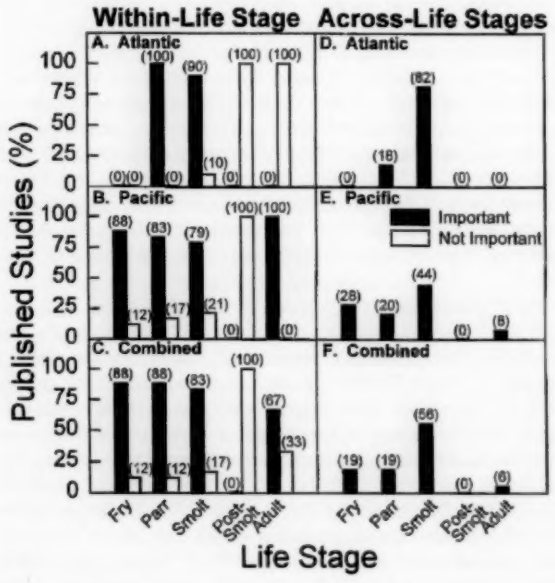


Fig. 2. Percent of studies in which predation was judged important or not important within each life stage (A, B, C) and across life stages (D, E, F) for studies published in nine journals between 1959–1996 that focused on Atlantic salmon (A, D), Pacific salmon (B, E), and all salmon combined (C, F). Dark bars are the studies in which predation was judged to be important by the author(s) of the study and light bars are those in which predation was judged to be not important. Numbers over the bars represent the percent of studies in which predation was judged important or not important. Life stage determination, i.e., fry, parr, smolt, post-smolt, adult, and the importance of predation was based on the author's classification.



evaluating the direct effects of predation, percent importance within each life stage (Fig. 2A–2C), and percent importance over all life stages (Fig. 2D–2F) were calculated for Atlantic salmon (Fig. 2A, 2D), Pacific salmon (Fig. 2B, 2E), and combined salmonids (Fig. 2C, 2F). Specifically, in 10 of the 14 prey taxa-life stage comparisons, more authors considered predation important than not important (Fig. 2A, Atlantic salmon parr, smolt; Fig. 2B, Pacific salmon, fry, parr, smolt, adult; Fig. 2C, combined salmonids, fry, parr, smolt, adult). For Atlantic salmon, within each life stage, predation was judged important in all or most studies undertaken at the parr and smolt stages and none at the post-smolt and adult stages (Fig. 2A). Across all life stages, 82% of all Atlantic salmon studies in which predation was judged to be important focused on the migratory smolt stage (Fig. 2D). Similarly, examining importance within each life stage for Pacific salmon, authors of 79–100% of all studies undertaken at the fry, parr, smolt, and adult life stages found predation to be important (Fig. 2B). Across life stages, 44, 28, and 20% of the studies on Pacific salmon in which predation was judged to be important occurred at the smolt, fry, and parr stages, respectively (Fig. 2E). Similarly, for combined

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salmon, predation was more often important than unimportant for early freshwater stages, i.e., fry, parr, smolt, and the older, freshwater adult stage but unimportant for the marine post-smolt stage (Fig. 2C). For all salmonids combined, over half of the studies in which predation was judged important focused on the transitional smolt stage (Fig. 2F).

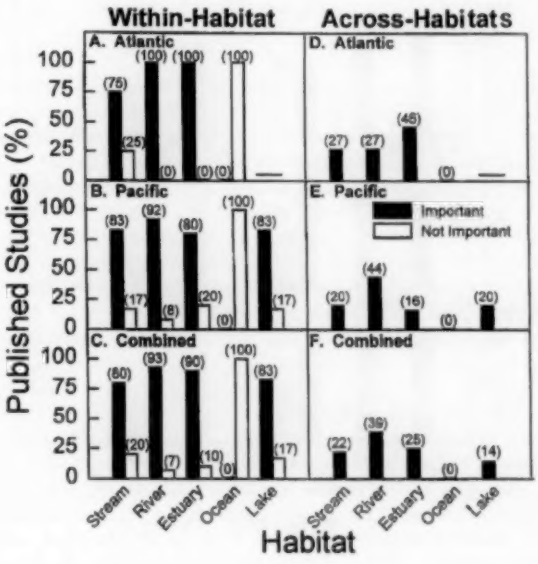
Predation is an important process for most life stages. However, some combination of circumstances, possibly related to aggregation, appears to make the smolts especially vulnerable. As salmon prey move down the river in large numbers, in many years and many systems, smolts probably swamp predators, quickly bypass sedentary predators, and escape spatial and temporal overlap with mobile predators thereby minimizing predation. However, in those years when overlap occurs, predation on densely concentrated smolts within the confines of the river corridor can be substantial if a gauntlet of predators is waiting downstream. Smolt vulnerability may also be affected by physiological challenges at the fresh–saltwater interface, human modifications of the river especially dams, and poor local adaptation common in many restoration and stocking programs.

Habitat

In 11 of 14 possible prey taxa–habitat combinations, more authors considered predation to be important than not important (Fig. 3A, Atlantic salmon, stream, river, estuary; Fig. 3B, Pacific salmon; and Fig. 3C, combined salmonids, stream, river, estuary, lake; data not available for Atlantic salmon-lake). For Atlantic salmon, within each habitat, the authors of 75–100% of the studies undertaken in the freshwater stream, river, and partially freshwater estuary habitats judged predation to be important (Fig. 3A). However, predation was not considered important for any studies on Atlantic salmon in the ocean (Fig. 3A). Over all Atlantic salmon habitats, almost twice as many studies in which predation was important were undertaken in the estuary habitat (47 vs. 27, 27%; Fig. 3D). For Pacific salmon, within each habitat, 80–92% of authors concluded that predation was important in the stream, river, estuary, and lake habitats (Fig. 3B). Across all habitats, for Pacific salmon, more studies in which predation was judged important were undertaken in the river (44 vs. 20, 20, 16; Fig. 3E). Similarly, for all salmonids combined, predation was judged more often important than unimportant in all habitats except the ocean (Fig. 3C); more than half of all studies in which predation was judged important (64%) occurred in the combined river and estuary habitats through which salmon move seasonally (Fig. 3F).

Salmon using the early, freshwater habitats and especially the transitional river/estuary are especially vulnerable. Clearly, smolts that move through the river into the estuary will be at risk in these habitats for the reasons described above. In the future it would be helpful to discriminate between true riverine habitats and hydropower dam tailraces and reservoirs. Many "riverine" studies are associated with manmade alterations and as such represent a very different type of habitat. When means and variances of survival from the literature were compared for five species of Pacific salmon to assess the contribution of the freshwater and marine habitats in recruitment variation, differences were observed across species, habitat, and life stage. In this study, both freshwater and marine habitats contribute substantially to overall mortality and interannual variability in recruitment (Bradford 1995). In my review, predation was more important in freshwater systems possibly because more salmon are confined in less space. Predation is certainly less studied in marine systems and also may be less important there although predation on salmon may simply be more difficult to document in the ocean. However, to draw any meaningful conclusions, we need to follow a cohort through an array of habitats using a rigorous comparative design.

Fig. 3. Percent of studies in which predation was judged important or not important within each habitat (A, B, C) and across habitats (D, E, F) for studies published in nine journals between 1959–1996 that focused on Atlantic salmon (A, D), Pacific salmon (B, E), and all salmon combined (C, F). Dark bars are the studies in which predation was judged to be important by the author(s) of the study and light bars are those in which predation was judged to be not important. Numbers over the bars represent the percent of studies in which predation was judged to be important or not important. The determination of habitat, i.e., stream, river, estuary, ocean, lake, and the importance of predation was based on the author's classification.



Predator taxa, method, and spatial scale

In all prey taxa – predator taxa combinations except one, more authors considered predation to be important than not important for Atlantic salmon (Fig. 4A, fish, bird), Pacific salmon (Fig. 4B, fish, bird, mammal), and combined salmonids (Fig. 4C, fish, bird, mammal). When mammals preyed on Atlantic salmon, predation was equally likely and unlikely to impact the prey population (Fig 4A). Most of the studies that judged predation to be important across all predator taxa examined fish predators (Fig 4D, Atlantic salmon, 64%; Fig. 4E, Pacific salmon 76%; Fig. 4F, combined, 72%). Piscivores like fish that coexist in the aquatic habitat with salmon 100% of the time may have a greater impact on

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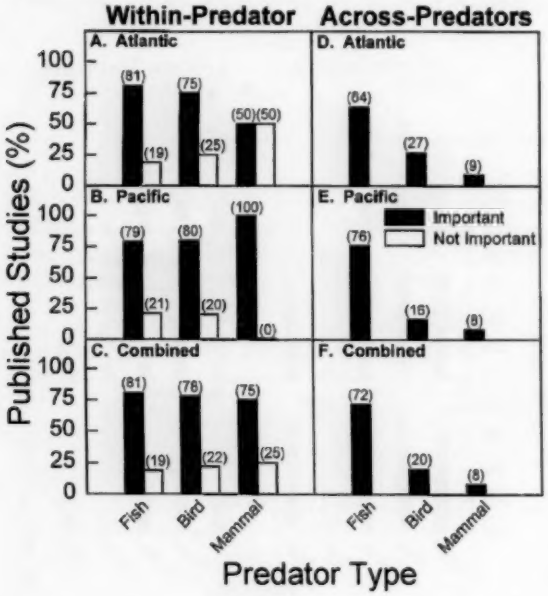
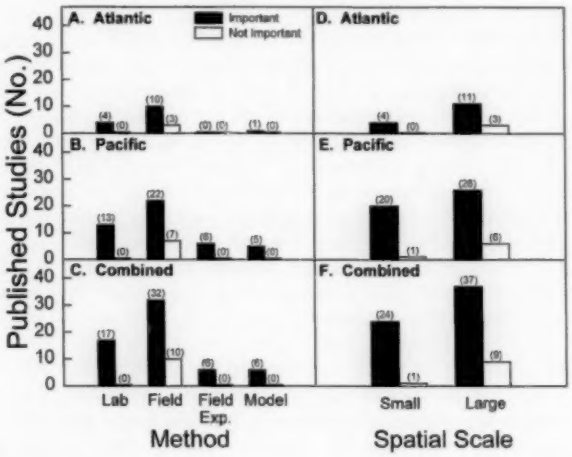
Fig. 4. Percent of studies in which predation was judged important or not important within each predator taxa (A, B, C) and across predator taxa (D, E, F) for studies published in nine journals between 1959–1996 that focused on Atlantic salmon (A, D), Pacific salmon (B, E), and all salmon combined (C, F). Numbers over the bars represent the percent of studies in which predation was judged to be important or not important. Dark bars are the studies in which predation was judged to be important by the author(s) of the study and light bars are those in which predation was judged to be not important.



salmon prey than bird or mammal predators. However, a bias may have been introduced by focusing primarily on fish journals. Across predator taxa comparisons would provide valuable insights on this difference.

Within each method, i.e., laboratory, field, field experiments, and models, more authors judged predation to be important than not important in the 11 taxa-method combinations for which data were available (Fig. 5A, Atlantic salmon, lab, field, model; Fig. 5B, Pacific salmon, lab, field, field experiments, model; Fig. 5C, all methods). More studies in which predation was judged important were undertaken with field surveys (Fig. 5A–C). More authors judged predation to be important than unimportant in their systems in all six combinations of spatial scale and prey taxa (two scales, three taxa, Fig. 5D–F). Overall, more studies in which predation was important occurred at the larger, meso-, site/reach scale (Fig. 5D–F). Scale issues, important to both ecology and management, require focused, explicitly designed studies. Both Atlantic and Pacific salmon, as migratory taxa, integrate across scales. Consequently, salmon are model systems in which to examine this issue as both small- and large-scale investigations are needed. Future research should address what is the right scale for each study question and how we can scale up to generalize from site to-basin. With rigorous, focused examinations, salmonid

Fig. 5. Number of studies within each methodological category (A, B, C) in which authors judged predation to be important or not important for Atlantic salmon (A), Pacific salmon (B), and all salmon combined (C). Number of studies in which authors judged predation to be important or not important related to two spatial scales (D, E, F) for Atlantic salmon (D), Pacific salmon (E), and all salmon combined (F).



systems can help us draw some generalities relative to these issues.

Key factors

To examine if the state of specific factors could provide insights into when predation is or is not important, I examined the number of studies in which authors judged each of the thirteen factors to be influential. This number ranged from three studies for prey behavior to 45 studies for overlap representing 7–100% of the total 45 studies (Fig. 6A). Both when predation was and was not judged to be important, the factors most often evaluated as influential were overlap (45, 100%), and abiotic factors (23, 51%; Fig. 6A). From 8 to 14 of the 45 studies in which predation was quantitatively assessed (18–31%) examined the remaining factors, predator species (14, 31%), morphometry (13, 29%), heterogeneity (13, 29%), season (13, 29%), predator behavior (11, 24%), prey species (10, 22%), community (10, 22%), predator number (9, 20%), size (8, 18%), and prey number (8, 18%; Fig. 6A). Less than 10% of the studies examined the role of prey behavior (3, 7%; Fig. 6A). A similar pattern emerged when all factors examined, both influential and uninfluential, were viewed (Fig. 6B) probably because the majority of authors (67–100%) only reported or discussed a factor when it was influential (Fig. 6C). Thus, less than a third of these quantitative predation studies examined the role of factors that could help explain the complexity of the predator prey interaction, provide insights into the prevalence of this biotic process across systems, and draw generalities about predation on salmonids through space and time.

If some pattern of influential factors defines the circumstances under which predation is important, then we would expect to see a different combination of influential factors when predation is important compared to when predation is

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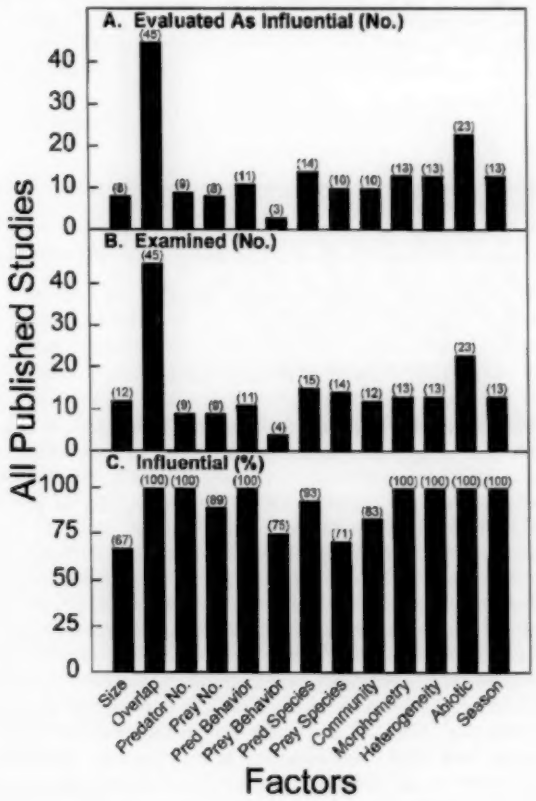
Fig. 6. (A) Number of all studies published in nine journals between 1959–1996 in which authors judged each of thirteen factors to be influential relative to predation on Atlantic and Pacific salmon. (B) Number of all studies in which authors examined each factor. (C) Percent of all studies in which the examined factor was judged influential. These factors included (1) predator–prey size ratio, (2) spatial and (or) temporal overlap, (3) predator number, (4) prey number, (5) predator behavior, (6) prey behavior, (7) predator taxa, (8) prey taxa, (9) community structure, (10) system morphometry, (11) spatial heterogeneity, (12) abiotic factors, and (13) seasonal influences. Both studies in which predation was and was not judged important are included.



not important. Indeed, different patterns do emerge (predation important, Fig. 7A, 7B; predation not important, Fig. 7C, 7D). When predation was judged to be important (Fig. 7A, 7B), a pattern similar to the previously described overall pattern of factor influence (Fig. 6A) was observed (Fig. 7A). In addition, in a few instances when predation was judged important, prey size, prey number, prey behavior, predator and prey taxa, and community structure were judged not influential (Fig. 7B). On the other hand, when predation was judged not important (Fig. 7C, 7D), few of these factors were evaluated either as influential (Fig.7C) or not influential (Fig. 7D). Because the role of so many factors was not evaluated and reported across the range of systems, the circumstances under which these variables influence the predator–prey process is difficult to assess and our understanding of how these systems and this process vary across space and time is severely limited.

Some factors were more commonly studied than others, and some factors, like overlap and abiotic effects, were more often associated with importance. The presence of more influential factors in studies in which predation was judged to be important may reflect real ecological differences or this trend may be related to a more rigorous study design in studies that report evidence of predation. Alternatively, this trend may simply be related to a methodological bias towards reporting only positive results. Clearly, a paucity of data is available in published studies to judge why predation is important in some systems but not others.

Approach

Because experimental manipulation, control, and replication are not generally options to study large-scale patterns like predation on migratory salmonid prey, other approaches must be used to effectively investigate circumstances under which this process is important. One way to test if select abiotic and biotic variables influence the strength of the predator–prey interaction is to collect similar types of data under comparable conditions in collaborative studies guided by multiple, falsifiable hypotheses (*a*) in the same system across years, (*b*) in different systems in the same year, or (*c*) in larger drainages, across basins. This approach uses nature as a laboratory to test relationships between select abiotic and biotic factors and the strength of predation across a gradient of natural systems and can yield valuable insights in the future. However, in the papers reviewed here, potentially important variables were not identified *a priori* and standardized data were not collected and reported. A second approach to examining these complex natural patterns is to test these same hypotheses with a rigorous, focused, multivariate analyses using existing multi-system data guided by *post hoc* hypotheses (Scheiner 1993). As my analyses showed, little consistent data on relevant factors are reported in the publications reviewed here. But if unpublished data are available from these authors, a reanalysis may be possible in the future. A third method to test relationships between patterns and processes in large, complex, natural systems, is the synthesis of results across studies using meta-analysis or the presence–absence type of comparative review undertaken here. Unfortunately, adequate information was not available in existing publications to use the meta-analytical approach, the pros and cons of which have been reviewed elsewhere (Gurevitch and Hedges 1993). However, the synthesis of the importance and unimportance of predation across studies, as described above, was possible.

Several problems exist with the type of review undertaken in this study. First, although the review of predation papers was fairly complete, the sample was non-random. Second, possible bias existed because negative results may not be equally represented in the peer-reviewed literature. Furthermore, my sample size was small and studies were unreplicated. Fourth, results were dichotomously categorized as either important or not important. Data on the magnitude of the effect were not incorporated because not enough detail was present in most publications as written. Fifth, great

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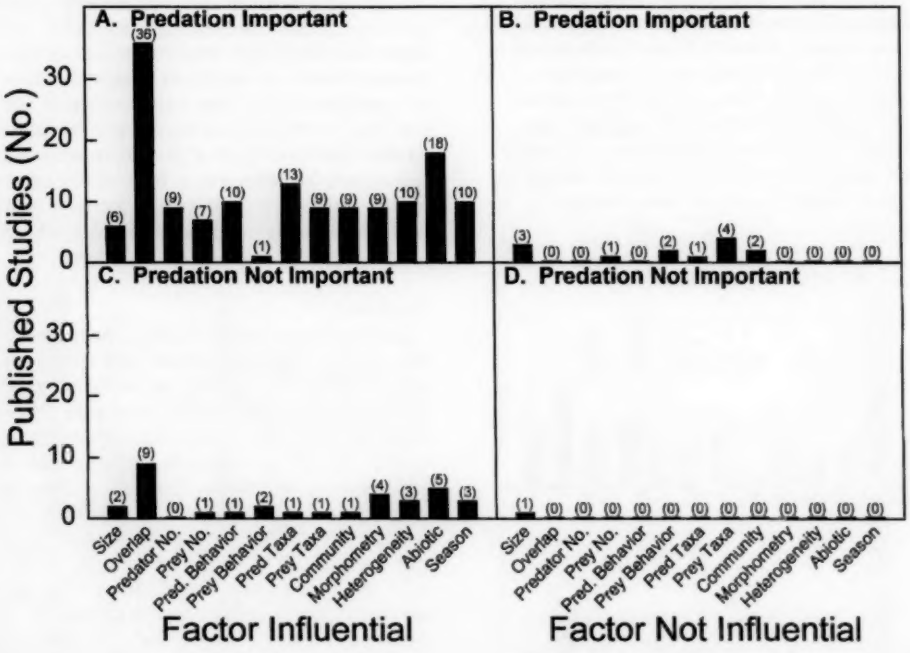
Fig. 7. Number of studies in which predation was judged important (A, B) or unimportant (C, D) published in nine journals between 1959–1996 in which authors evaluated each of thirteen factors as influential (A, C) or not influential (B, D) relative to predation on Atlantic and Pacific salmon.



subjectivity existed relative to the criteria for importance. Namely, my classification was based only on the author's judgment. Thus, variability existed in the rigor of the studies reviewed even though each counted equally. Sixth, effort expended to study each variable varied radically. Nevertheless, the distribution of this differential effort was, in itself, informative. Finally, predators can have important effects without killing or otherwise altering large numbers of prey. Hence, my somewhat arbitrary demarcation of intensity or importance can be misleading relative to the total role this process plays in determining natural patterns. Even given these limitations, generalities can be drawn. Perhaps most importantly, the majority of studies do not address or at least publish adequate data on the suite of confounding factors that might help us understand variation in predation across systems. If we are to optimize what we learn from field studies, we need a focused, comparative approach where data on a set of standardized factors are collected in a similar way regardless of the specific predation-oriented question being addressed. Then each system can be used as a replicate or at least a comparable data point in a larger analysis (Table 3).

Future directions

Several issues identified here merit further investigation. First, quantifying the pattern of heterogeneity and overlap is critical to our understanding of predation. The outcome of predation in a temporally fluctuating community is intriguing because outmigration necessarily concentrates fish and makes potential prey extremely vulnerable to predation, albeit in a potentially unpredictable way. In systems where a healthy, coevolved population of Atlantic salmon has persisted, does the population consistently escape predation each year or are there sustained salmon populations that are periodically or consistently decimated? Second, evolutionarily, what are the implications of the decoupling of predator–prey systems associated with salmon stocking and enhancement? Is there a relationship between the length of species associations and the strength of their interactions, a question of particular important for restoration efforts? Third, how do human impacts alter the predator–prey process? Can we compare pristine and impacted systems to understand how landscapes and communities where Atlantic salmon are found have changed relative to human impacts (Power et al. 1996)? Can we test how dams, modified hydrographs, and land modifications affect instream structure, fragmentation, productivity, and consequently predator–prey interactions? Finally, a large number of independent Atlantic salmon populations exist and these populations can provide us with a model system to understand how to document, explain, and predict site-to-site and year-to-year natural variation.

In summary, because predators can seriously affect potential salmon prey, understanding the context or combination of conditions that determine when this process affects the prey community is critical. By collecting standardized information guided by hypothesis testing, we can start to put together a conceptual framework that defines in what context predation is important. Furthermore, documenting variation in these conditions across years and systems can help integrate data that advances our basic ecological understanding while providing information for wise management and effective conservation.

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Table 3. Factors to be measured in future Atlantic salmon predator prey studies to enhance our understanding of when and why predation is important or not important across systems.

Size		**Overlap**	
Predator, X, SE, Range		Time of predator movements	
Prey, X, SE, Range		Time of prey movements	
Alternative Prey, X, SE, Range		Duration of overlap	
Numbers			
Prey population size,		*Predator population size*	
Present, 5-year mean, historical		Present, 5-year mean, historical	
Alternative prey			
Behavior		**Taxa**	
Predator and prey movements, microhabitat use, foraging		Predator and prey taxa present, relative abundance, size, diet	
Morphometry			
Stream order	Length	Mean width	Mean depth
Channel units/dimensions	Estuary dimensions	Bank geometry	Riparian zone
Sinusosity	Land use		
Abiotic			
Hydrograph	Discharge	Substrate	Temperature
Other			
Scale of investigation	Heterogeneity	Human impacts	History of stocking

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Appendix

Table A1. Papers used in databases 2 and 3.

Database	Author(s) (Year)	Author(s) (Year)
2 and 3	Beamish et. al (1992)	Beamish and Neville (1995)
	Beauchamp (1995)	Beauchamp et al. (1995)
	Buchanan et al. (1981)	Carss et al. (1990)
	Dolloff (1993)	Feltham (1995)
	Fresh and Schroder (1987)	Gunnerod et al. (1988)
	Harmon et al. (1994)	Heggenes and Borgstrom (1988)
	Hvidsten and Mokkelgjerd (1987)	Hvidsten and Lund (1988)
	Jones and Geen (1977)	Larsson (1985)
	Montevecchi et al. (1988)	Mossman (1958)
	Patten (1962)	Peterman and Gatto (1978)
	Petersen (1994)	Poe et al. (1991)
	Rieman et al. (1991)	Roos (1959, 1960)
	Ruggerone (1986)	Ruggerone and Rogers (1992)
	Schulze (1996)	Tabor et al. (1993)
	Thompson and Tufts (1967)	Thorsteinson (1962)
	Vigg et al. (1991)	Ward and Slaney (1990)
	Wood (1987*a*, *b*)	
3 only	Bugert and Bjornn (1991)	Bugert et al. (1991)
	Gadomski and Hall-Griswold (1992)	Gadomski et al. (1994)
	Ginetz and Larkin (1976)	Gregory (1993)
	Gregory and Levings (1996)	Handeland et al. (1996)
	Hargreaves and LeBrasseur (1985)	Hargreaves and LeBrasseur (1986)
	Healey and Reinhardt (1995)	Huntingford et al. (1988*a*,*b*)
	Jarvi (1989)	Magnhagen (1988)
	Martel (1996)	Mesa (1994)
	Parker (1971)	Patten (1971)
	Petersen and DeAngelis (1992)	Petersen and Gadomski (1994)
	Petersen et al. (1994)	Ryer and Olla (1996)
	Sylvester (1973)	

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Diseases and parasites in wild Atlantic salmon (*Salmo salar*) populations

Tor A. Bakke and Philip D. Harris

Abstract: The ecology of infectious diseases in wild and managed salmon populations is reviewed. Few pathogens have caused significant disease epidemics in the wild, and although parasites of returning adults are best documented, diseases among parr (e.g., *Gyrodactylus salaris*) are probably most important. The greatest diversity of parasites is known from the marine phase but few are likely to be significant pathogens, although conclusive evidence is lacking because diseased salmon cannot be tracked. The importance of stress as an immunosuppressant of fishes in degraded habitats is discussed. In addition, releases and restocking have probably also reduced the genetic disease resistance of wild fishes. We note that myxozoans, furunculosis, *G. salaris*, and sea lice are the pathogens most likely to threaten wild and managed salmon stocks in future. Despite abundant research on pathogens of farmed salmon, little is known of their impact on wild or managed stocks and an adequate theoretical framework for salmon disease epidemiology is urgently needed before disease becomes a limiting factor in salmon conservation.

Résumé : On examine l'écologie des maladies infectieuses chez les populations sauvages et issues du repeuplement. Peu de pathogènes ont causé d'importantes épizooties dans le milieu naturel, et, bien que les cas de parasitisme chez les adultes en montaison soient les mieux documentés, les maladies touchant les tacons (p. ex. *G. salaris*) sont probablement les plus importantes. C'est dans le milieu marin qu'on observe la plus grande diversité de parasites, mais peu de parasites risquent d'être d'importants pathogènes, même si nous manquons de preuves concluantes en raison du fait que les saumons malades ne peuvent être suivis. On traite aussi de l'importance du stress comme agent immunosuppressif chez les poissons qui vivent dans des habitats dégradés. De plus, les lâchers et le repeuplement ont probablement aussi réduit chez les poissons sauvages la résistance génétique aux maladies. Nous indiquons que les myxozoaires, la bactérie responsable de la furonculose, *G. salaris*, et les poux de poisson sont les pathogènes qui menaceront le plus les stocks de saumons sauvages et issus du repeuplement dans l'avenir. Malgré les nombreuses recherches sur les pathogènes des saumons d'élevage, on sait peu de choses de leur impact sur les stocks sauvages et issus du repeuplement, et il est urgent que nous disposions d'un cadre théorique adéquat pour l'épidémiologie des maladies du saumon avant que ces maladies deviennent un facteur limitant dans la conservation du saumon.

[Traduit par la Rédaction]

1. Introduction

Salmon are one of the most intensively studied of teleosts, with records of epidemic disease in wild populations dating back to furunculosis outbreaks in the late 19th century (Emmerich and Weibel 1894). Over the past 30 years many books have described the pathogens of farmed salmon (e.g., Post 1987; Bruno and Poppe 1996). This review however has a different purpose: to synthesise current knowledge of the ecology and epidemiology of infectious disease in wild Atlantic salmon (*Salmo salar*) populations. We are particularly concerned to identify those diseases that could influence population dynamics and growth in natural environments. The ecological and genetic consequences of salmon diseases and the impact of human influences (both direct management and indirect environmental factors) will also be discussed. Finally we review the impact of salmon farming on disease in wild fishes and speculate on future potential disease problems in the natural environment.

This review is written from an ecological perspective, introducing epidemiological concepts (e.g., Anderson 1982; Anderson and May 1978, 1979; Smith 1994; Grenfell and Dobson 1995), which have been slow to spread to the study of aquatic diseases (e.g., Dobson and May 1986). However, veterinarians, fishery managers, and ecologists differ significantly in their approach to infectious disease. For example, a paradigm of veterinary and human medicine has been that, for a particular disease, Koch's postulates can be satisfied (e.g., Hill 1965; Evans 1976). In aquatic wild organisms, this may simply not be possible: the pathogenicity of infectious agents may be so great that infected fishes die and disappear before they can be detected. This does not mean that their disease potential should be ignored. Indeed, Hill's (1965) criteria cannot be met for either the spread of furunculosis (Johnsen and Jensen 1994) or for the current epidemic of *Gyrodactylus salaris* (Halvorsen and Hartvigsen 1989; Johnsen and Jensen 1992), and in the latter case, this failure could arguably have contributed to the slow response of the Norwegian establishment to the emerging problem.

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T.A. Bakke.[1] Zoological Museum, University of Oslo, Sars Gate 1, N-0562, Oslo, Norway.
P.D. Harris.[2] Schools of Continuing Education and Biological Sciences, University of Nottingham, Nottingham NG7 2RD, U.K.

[1]Author to whom all correspondence should be addressed.
e-mail: t.a.bakke@toyen.uio.no
[2]In alphabetical order.

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We have therefore followed a precautionary principle, considering as potential pathogens in the natural environment those organisms that can cause disease in salmonid aquaculture or under experimental conditions and those organisms which are closely related to, or have a similar life history to, known pathogens.

Very few pathogens have had significant impacts on wild salmon populations and the spread of disease from farm to the wild remains a rare phenomenon, despite the current extent of salmonid aquaculture. Historically, only furunculosis (Inglis et al. 1993), a few other bacterial infections, ulcerative dermal necrosis (UDN; Roberts 1993), and *Gyrodactylus salaris* (Johnsen and Jensen 1991) have caused widespread conspicuous epidemics in wild populations. This does not necessarily mean that infectious disease is rare in natural populations (Kinne 1984; Munro et al. 1983; Lester 1984). It is often very difficult to quantify the effect of a pathogen on host population dynamics. For example, the aquatic fungus *Saprolegnia* is common on spawning adult salmon and can kill fishes (Pickering and Willoughby 1982). Nevertheless, it appears unable to infect healthy fishes, being a secondary pathogen exploiting weakened hosts. Similarly, when *G. salaris* was first described from Norwegian salmon (Johnsen 1978), it was not recognized as a primary pathogen because of its co-occurrence with *Saprolegnia*. The complex etiology of diseases in the wild is especially well demonstrated by UDN. Originally described as salmon disease and noted for its impact in the late 19th century (Roberts 1993), this disease then disappeared until the 1960s. The temporal and spatial spread of this disease (Roberts 1993) is strongly reminiscent of an infectious agent (Anderson 1982); however, despite intensive study, the causative agent remains unknown.

2. Parasite population ecology

2.1. Individual and population effects of parasitism

All parasites utilize energy otherwise available for host growth, survival, and reproduction and are important determinants of animal community structures (Minchella and Scott 1991). Many studies have shown sublethal effects on individual host survival, especially when it is advantageous to engineer the host's death to ensure transmission (see e.g., Lester 1977; Crowden and Broom 1980; Halvorsen and Andersen 1984; Milinski 1984; Rodger 1991; Bylund and Andersen 1994). Detecting the effects of parasitism in wild host populations, can however be very difficult (Anderson and Gordon 1982). To detect with confidence mortality due to selective predation of digenean-infected sticklebacks, Gordon and Rau (1982) sampled about 100 fishes per month; this would be quite impractical in most salmonid populations. Parasites and pathogens may therefore be overlooked as sources of mortality or sublethal morbidity, especially in juvenile fish populations (Gardiner and Geddes 1980; Clers 1993; Brabrand et al. 1994) from which dead and diseased individuals rapidly disappear. Disease is not thought to be important in salmonid population dynamics, except when conspicuous epidemics occur, and salmonid populations are instead regulated by density-dependent processes within the natal river (Elliott 1994; Elliott and Hurley 1998; Mills 1989). However, some evidence suggests that disease might regulate salmonid populations more generally. Clers (1993), for example, showed by modeling that *G. salaris*, infecting parr, could limit salmon population growth, while Levy and Wood (1992) felt that the cyclic abundance of sockeye salmon could best be explained by a pathogen. The life history of Atlantic salmon would blur the effects of disease epidemics and make them harder to detect; however, this lack of evidence does not mean that diseases play no part in wild salmon population dynamics.

Even small effects of parasitism may be critical in the wild, as reduction of parr growth by only a few percent may defer smolting by an entire year (see Marschall et al. 1998). The effect of a parasite on salmon reproductive rate might then be quite severe, although effects on population size and indeed the host itself may be undetectable. A further point to consider is the evolutionary cost of parasitism (Lehmann 1993; Grenfell and Dobson 1995). The production of xenobiotic chemicals is selected against when parasitism is relaxed (Behnke 1990) suggesting that excessively resistant hosts have their growth rate reduced as resources are diverted inappropriately to the immune system. The complexity and polymorphism of the immune system suggests that it is indispensable for survival (Price 1985; Wassom et al. 1986; Chevassus and Dorson 1990; Bakke et al. 1990; Gjedrem et al. 1991) and argues for the importance of parasitism as a selective force in natural salmon populations.

2.2. Microparasites versus macroparasites

An important distinction exists between microparasitic pathogens and macroparasites. Microparasites (e.g., viruses, bacteria, some protozoans, and *G. salaris*) reproduce in situ on the host, have small biomass, reproduce rapidly, and tend to induce lasting immunity (Anderson and May 1979). Macroparasites (including fish lice, tapeworms, nematodes, and some protozoans and fungal pathogens) have low reproductive rates, with long generation times and larger body size, and dispersal of young away from the host. The immune response may be less effective and infestations tend to be persistent (Dobson and May 1986). Figure 1 demonstrates that the proportion of macroparasites recorded from salmon in the literature is larger in wild populations, in contrast to microparasites, which dominate published diversity in cultured fishes. This can be explained by high host densities, simplified ecological conditions, and short residence time, favoring transmission of directly infecting microparasites, and by the greater ease of study of cultured fishes. These conditions seem also to favor the occurrence of fungi that are most frequently recorded in farms.

2.3. Parasites and pathogens have aggregated distributions

A few hosts carry the majority of the parasite population and most hosts are barely infected (Crofton 1971; Pennycuick 1971; Anderson and May 1978). Several factors are responsible for this. Microparasites reproduce in situ and therefore become highly aggregated. On the other hand, selective mortality, culling heavily infected fishes, reduces aggregation. Other factors may be environmental. Some parasites have extremely local distributions and spread slowly, so that spatially isolated metapopulations (e.g., parr in a riffle) may be heavily infected while neighboring meta-

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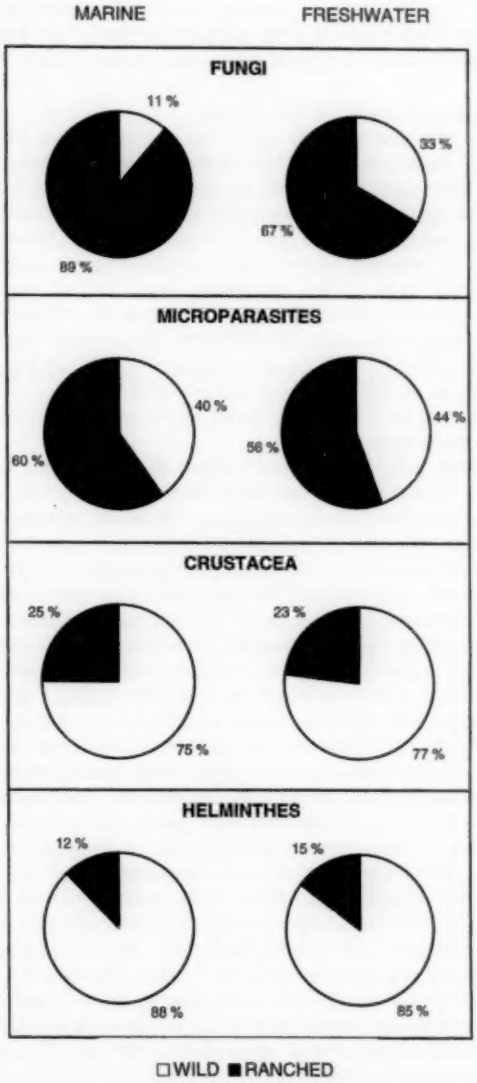
Fig. 1. The proportion of species of infectious agents infecting ranched and wild Atlantic salmon under freshwater and marine conditions. The macroparasites are represented by the helminths and crustaceans, the microparasites by the virus, bacterians, and protoctistans. The results indicate that constrained conditions in farms favor the microparasitic life strategy for fungi. (The data are based on a literature survey of infectious pathogens reported from the Atlantic salmon.)



populations remain uninfected. Aggregation may also be related to the relative susceptibility of hosts, which is usually genetically controlled (Chevassus and Dorson 1990; Wakelin 1994), and at least as important as physiological and ecological factors in generating patchiness. Preliminary studies (Bakke et al. 1990; Bakke and MacKenzie 1993; Gjedrem et al. 1991) have shown genetic heterogeneity in disease resistance among salmon and other salmonids (Bakke et al. 1996), but the importance of this phenomenon in the field has not been considered and should be investigated. Heterogeneity of resistance is a paradigm of *G. salaris* epidemiology, with Norwegian salmon considered susceptible while Baltic salmon are resistant (Mo 1994). Our experimental studies have shown considerable heterogeneity between salmon stocks (see Figs. 2A, 2B), also Norwegian stocks, as well as within single stocks (see Figs. 2A, 2B) of both Norwegian and Baltic salmon. The figure demonstrates that both major stocks are susceptible to the Norwegian strain of *G. salaris* and acquire a response against the infection after the same time period, but with the Norwegian salmon most susceptible to parasite reproduction.

2.4. Stable versus unstable population dynamics

The microparasite–macroparasite demarcation profoundly affects the stability of host–pathogen interactions (Anderson and May 1979). Dispersal away from the host and long, complex life cycles favour stability, with parasite populations often limited by density dependent processes such as competition (Anderson 1982). Macroparasites, although sometimes causing conspicuous harm to heavily infected individuals, usually have negligible effects on wild host populations and often remain stable through time (e.g., Kennedy 1981; Amundsen et al. 1997). In contrast, microparasites lack stability, their populations oscillating between virtually extinct and dangerously large with alarming rapidity. Populations of *G. salaris*, for example, can vary in size by several orders of magnitude over periods of a few weeks, while the host population remains constant (Jansen and Bakke 1993*a*, 1993*b*; Bakke et al. 1990, 1996). Thus microparasites, which may be very difficult to detect, and which as individuals are negligible, are of overwhelmingly greater importance as pathogens, as potential regulators of host population size, and as selective agents.

Within salmon farms a number of macroparasites can be pathogenic (Bristow and Berland 1991*a*; Rodger 1991). Fish lice are perhaps the best examples (cf. Boxshall and Defaye 1993; Heuch 1996), illustrating that ultimately the microparasite–macroparasite distinction is artificial. Within sea pens dispersal does not take place efficiently, allowing reinfection. Low juvenile mortality greatly shortens parasite generation time and the population dynamics become increasingly unstable and resemble those of a microparasite.

3. Cohorts and ecological groups of wild salmon

3.1. Salmon life cycles and parasites

Different stages of the salmon life cycle are both spatially and temporally separated in lotic and lentic freshwater systems and in marine coastal and pelagic areas, overlapping minimally. This has a prominent effect on the ecology of salmon–pathogen interactions (Zschokke 1880; Heitz 1920; Dogiel and Petroshevskij 1935; Margolis 1982*a*, 1982*b*; Soleng and Bakke 1997). Along a river system there are longitudinally restricted spawning redds; nonfeeding alevins (for which the oral route of infection is not available); fry, which disperse from the redd to individual territories and allow the early spread of infections through a riffle system; parr, which by their aggressive dominance behavior force

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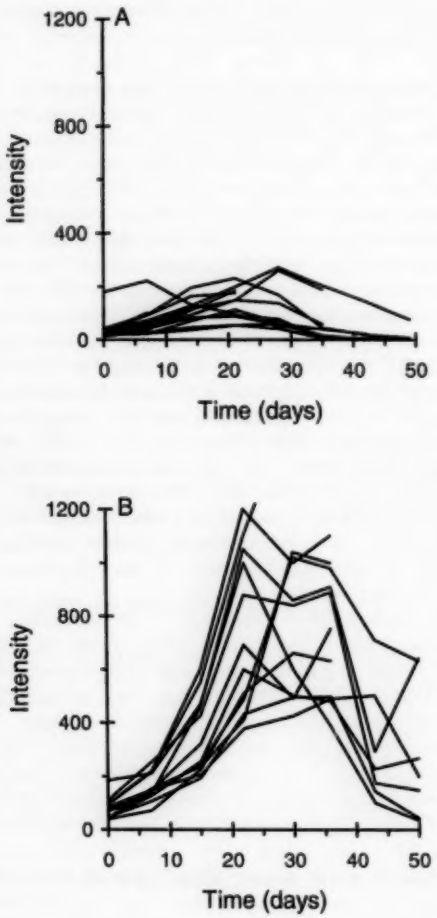
Fig. 2. Inter- and intra-populational heterogeneity is recorded in the susceptibility and resistance of Atlantic salmon to the Norwegian strain of *Gyrodactylus salaris*. (A) The course of infection of *G. salaris* on individually infected and isolated Baltic salmon from the River Neva, Russia (originals). (B) The course of infection of *G. salaris* on individually infected and isolated Norwegian salmon from the River Lierelva, south-east Norway (Bakke and MacKenzie 1993). (One line indicates one individually isolated fish, parasite numbers counted on anaesthetized fish; cf. Bakke et al. 1990).



the shoal to occupy larger and larger areas of the river, increasing opportunities for contraction and dissemination of disease; smoltifying parr, which undergo large physiological changes with consequences for their parasite burden; sea-running smolt, which move pathogens between parr patches and eventually carry them to the mouth of rivers; sea-migrating smolts, in which coastal parasites are aquired while freshwater parasites are lost; immature adults on the feeding grounds, able to ingest parasites in significant quantitities; returning adults, which disperse pathogens from the feeding grounds to the coastal areas; mature adults, which disperse pathogens upstream from the river mouth to the breeding sites; and kelts, which drifting seawards and heavily infected with opportunist pathogens may be particularly significant in the spread of disease (Soleng et al. 1997). Dwarf males may be continually present and, being immunosuppressed (Pickering 1987, 1989), may harbor a disproportionate total of the pathogens present in the population, while in landlocked salmon populations, only freshwater pathogens can survive. A literature survey of infectious agents reported from Atlantic salmon demonstrated a minimum of 225 species. Among those the digeneans and cestodes dominate the macroparasite groups, while bacteria and protoctistans dominate the microparasites (Table 1).

3.2 Juvenile stages in freshwater

The life span of each stage varies dramatically. That of eggs in redds, alevins, and fry is short, only a few months in total. Few pathogens, with the exception of some viruses and the opportunist hyphomycete *Saprolegnia* sp., are sufficiently mobile to infect spatially separated redds. Some vertically transmitted bacteria can overcome this problem by colonizing eggs during, or shortly after, laying and may cause early life stage mortality (Sauter et al. 1987). Lysozymes restrict the range of pathogens able to infect eggs, although some, for example *Renibacterium salmoninarum* (Yousif et al. 1994), and possibly *Piscirickettsia salmonis* (Larenas et al. 1996), can avoid neutralization by this defense mechanism.

Salmon parr have a variable lifespan, from 1 year in the south of the range (Nicieza et al. 1994) to 5 years in northern Norway and Canada. There may, therefore, be between 1 and 5 overlapping cohorts in a river, which greatly influences the possible dynamics of their pathogens. A parasite such as *G. salaris* might be expected to go extinct within small metapopulations of parr in the south of the host range, because of insufficient overlap between parr year-classes. Parr survivorship varies considerably with age (Rye et al. 1990; Clers 1994). In brown trout (*Salmo trutta*), a parasite infecting newly hatched fry can be 80% certain that its host will die within 20 days (Fig. 3A, recalculated from Elliott 1989*a*, 1989*b*, 1994) and must possess transmission and survival strategies to cope with this eventuality. Infection of 3-month-old parr, however (Fig. 3 B), gives a 70% chance that the host can be exploited for 3 months or more. This age-related difference is less dramatic for salmon (Figs. 3C, 3D; data recalculated from Mills 1989), possibly because detailed studies comparable to Elliott's (1989*a*, 1989*b*, 1994) studies of trout are not available. The basic reproductive rate, R_0, of a pathogen (Anderson 1982) infecting fry may need to be at least 20–100 to compensate for propagules infecting hosts which accidentally die of other causes. On the other hand, if infection is delayed the parr may already be unsuitable because of a preexisting infection. This trade-off, and its practical consequence when rivers are restocked, is poorly understood for any salmon pathogen.

3.3. The marine phase

Little is known about disease among marine salmon and the parasites/pathogens known from wild marine fishes are those larger macroparasites which probably cause least harm (e.g., Shulman and Shulman-Albova 1953; Polyanskii 1955; Pippy 1969*a*, 1969*b*, 1980; Hicks and Threlfall 1973;

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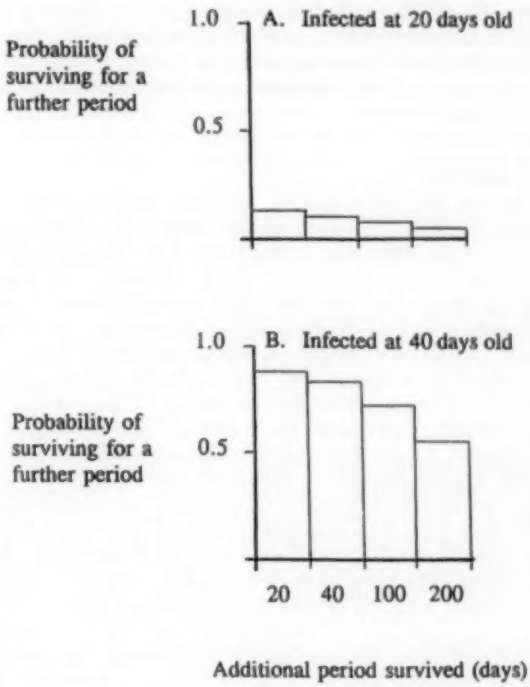
Table 1. The total number of species of infectious agents reported from wild and domesticated (ranched/hatchery) Atlantic salmon in both marine and freshwater habitats.

Group	Number of species
Virus	9
Monera	21
Protoctista	27
Animalia	
Hirudinea	3
Helminths	
Monogenea	11
Digenea	41
Cestoda	35
Nematoda	29
Acanthocephala	20
Crustacea	13
Mollusca	3
Acarina	2
Fungi	11
Total number	225

Note: Undetermined species are frequently reported but counted as one only if it represents the single record of a particular genus. The figures represent minimum numbers based on a literature survey.

Bristow and Berland 1991*b*; Holst et al. 1993; Mitenev 1993; Bristow et al. 1996). This reflects the more diverse environment, which juvenile salmon pass through on their way to the marine feeding grounds, offering opportunities for infection by parasites with complex multihost life cycles. It is also because the more virulent marine microparasites, if they exist, kill their hosts without trace. Sea pen culture has greatly increased our knowledge of marine pathogens, particularly revealing a diverse microparasite fauna. Viruses such as (ISA), known from ranched salmon in Norway (Thorud and Djupvik 1988), Nova Scotia (B. Dannevig, National Veterinary Institute, Oslo, personal communication) and most recently from Scotland, may occur naturally, but are sufficiently pathogenic to restrict transmission. Epidemics of ISA or other viral diseases among wild marine salmon are probably rare, because the density of salmon at sea is so low. However, this disease and others might impose an additional unseen mortality on smolts as they begin the marine phase (Uno 1990; Soleng et al. 1997). Olsen et al. (1997) describe rickettsial disease in smolts occurring only after seawater exposure in farms along the west coast of Norway; this may be a common pathogen of this life history stage but is only detected in net pens because of the difficulties of sampling migrating wild smolts. A similar situation may occur with the unidentified myxozoan associated with encephalitis of net pen reared salmon in Ireland (Frasca et al. 1998). Nothing is known of pathogens causing epidemic disease in wild marine salmon, but the fungus *Ichthyophonus hoferi* is almost ubiquitous among wild marine fishes and can cause major epidemics (Sindermann 1970; Møller and Anders 1986). At least one microparasite infecting marine salmon is therefore potentially capable of limiting host population size. The development of molecular (Mooney et al. 1995) and immunochemical probes will be very useful in determining the spectrum of pathogens to which marine fishes have been exposed.

Figs. 3A, 3B. Influence of host age on probability of successful completion of pathogen life cycle. (A) Probability of 20-day-old trout fry surviving for specified further periods following infection, to allow completion of the life cycle. (B) Probability of 40-day-old fry surviving for specified further periods following infection. Calculated from survival data for *Salmo trutta* in Black Brows Brook presented by Elliott (1989, 1994). Figure assumes that parasite does not adversely affect survival of fry.



4. Diseases of salmon (*Salmo salar*) in the wild — case studies

In this section we present an outline of the systematic groups to which salmon pathogens belong and identify aspects of their ecology which are of particular interest.

4.1. Viruses

Many viruses infect salmon within aquaculture facilities; viral infections of wild salmon are far harder to identify and to our knowledge there have been no reports of disease epidemics due to viruses in wild salmon populations. Viruses obviously exist within wild salmon populations, their frequency within aquaculture units reflects the importance of fish farms in sampling and amplifying pathogens in the natural environment. ISA, for example, presumably exists within the natural salmon population at low intensity but is not found because infected wild fishes die and disappear. Because salmon aquaculture is a relatively young industry,

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new viral infections frequently appear and continue to be identified, including for example the togavirus reponsible for pancreas disease (Nelson et al. 1995; McLoughlin et al. 1996, 1998). There is however no evidence for transfer of viral infections from farm to wild salmon populations, although viruses such as infectious pancreatic necrosis (IPN) may be frequently isolated from escaped salmonids (Bucke 1993). Endemic viruses may have considerable impact on young fishes (fry and parr) but have not been looked for in studies of wild salmon population dynamics. The introduction of molecular and immunological probes, allowing the disease history of individual fishes to be recreated in the absence of obvious symptoms, will help greatly in understanding the pattern of microparasitic pathogens to which salmon are exposed.

4.2. Bacteria

Salmon are susceptible to numerous bacterial diseases, some of which have been studied intensively (Austin and Austin 1987; Inglis et al. 1993). In the wild, disease epidemics have been caused by several bacteria, including *Renibacterium salmoninarum,* which caused epidemic bacterial kidney disease (BKD) in the Aberdeenshire Dee in the 1930s (Smith 1964). BKD is a serious and fatal systemic infection of both farmed and wild salmonids (Bruno 1986; Bruno and Poppe 1996) but knowledge of its etiology is nevertheless fragmentary. The bacterium may be a normal member of the gut flora (Austin and Austin 1987), which at times of stress migrates to the kidney and causes overt disease. Bucke (1993) was unable to isolate *R. salmoninarum* from over 3000 wild salmonids in Britain, although full details of the sampling regime used were not given. Of the numerous other bacteria known from salmon, only furunculosis is a serious pathogen of wild fishes. Although bacteria such as *Vibrio* species (*V. anguillarum* and Hitra disease, *V. salmonicida*), *Yersinia ruckeri* (responsible for enteric redmouth), and *Flexibacter* species (e.g., *F. columnaris*, responsible for columnaris disease) are well known from farm situations, there appear to be no records of outbreaks of these diseases in wild salmon. This may be because their pathogenicity is so great that infected fishes die before they can be sampled, or, perhaps more likely, because there are no transmission cycles between farmed and wild fishes.

4.2.1 Furunculosis

Furunculosis, caused by *Aeromonas salmonicida*, is one of the best known and most important diseases of salmonids and has been extensively reviewed (Austin and Austin 1987; Inglis et al. 1993; Johnsen and Jensen 1994). The pathogen was first detected in Europe (Emmerich and Weibel 1894) and North America at the end of the 19th century, causing epidemics in wild trout. The British epidemic within wild trout and salmon at the start of the 20th century was particularly well documented (Masterman and Arkwright 1911; Lund 1967; Austin and Austin 1987). It began in the southwest peninsula in 1911, spreading steadily north and eastwards to reach the important Scottish salmon rivers by the late 1920s. A similar pattern was observed in Norway following introduction from Denmark in 1964 (Lunder and Håstein 1990). In this case, the pathogen was eventually exterminated in 1969 (Håstein 1989). In both cases, the pattern of spread was characteristic of an introduced pathogen, eventually slowing down and losing pathogenicity as the bacterium became endemic.

A second phase began with epidemics in farmed marine salmon from the mid-1980s onwards. The marine form of *A. salmonicida* originated in Scotland, spreading to Norway in 1985 (Egidius 1987; figs. 5, 6), and since then it has become entrenched in marine farms (Håstein et al. 1989). Furunculosis spread from coastal fish farms with the numerous escapes and wild fish in 74 rivers had been infected by the end of 1992 (Johnsen and Jensen 1994). The taxonomy of *A. salmonicida* is controversial (Austin and Austin 1987) and relationships between marine and freshwater strains are not clear. It is interesting that observations in the early part of the century suggested that this pathogen could not colonize salmon in seawater. Thus, 1339 smolts collected from British estuaries in the 1930s were all uninfected (cited in Austin and Austin 1987).

Several ecological factors provoke concern for the potential impact of furunculosis spreading from farms to wild salmonids. Nese and Enger (1993) recovered viable *A. salmonicida* from salmon lice collected from within net pens and Costelloe et al. (1998) have recorded *L. salmonis* larvae derived from farmed salmon dispersing within an estuary. It would therefore be theoretically possible for *A. salmonicida* to transfer to migrating smolts or returning adults passing through estuaries. Smolt infected in this way would be almost impossible to track, while adults migrating upstream could pass furunculosis on to immature salmon in their nursery rivers. Escaped farmed salmon may also be a significant source of furunculosis infections in natural salmon populations (Johnsen and Jensen 1994). *Aeromonas salmonicida* can also infect other fish species, including cleaner wrasse (Austin and Austin 1987), coalfish, cod, and turbot (Willumsen 1990; Hjeltnes et al. 1995), although infections are short-lived and nonpathogenic (Hjeltnes et al. 1995). Additional studies using techniques such as PCR capable of detecting very small *A. salmonicida* populations should be urgently applied to determine the status of this pathogen on salmon and sea trout transiently residing in estuaries (McArdle et al. 1993; Mooney et al. 1995).

A most worrying aspect of *A. salmonicida* is its propensity to transfer plasmids conferring drug resistance between strains (Austin and Austin 1987). Sakai (1987) has noted exchange of protease genes between pathogenic and nonpathogenic strains, under circumstances similar to those occurring in river sediments. Since protease phenotype is an important determinant of virulence in *A. salmonicida,* this is clearly a potential source of new, genetically and ecologically distinct strains of the pathogen which could possibly infect wild salmon populations.

4.3. Protoctista

Many of the approximately 2420 species of fish-infecting protoctistans are serious pathogens (Lom and Dykova 1992). Some cause significant mortalities of salmon, while others are not primary pathogens or do not significantly affect the fish. None are known to be problems in wild salmon populations, although several species could become pathogens.

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4.3.1 Myxozoa

Myxozoans are well known for their distinctive propagules which are found within the fish's tissues, often in conspicuous cysts. Seven species infect Atlantic salmon.

Proliferative kidney disease (PKD), which affects most farmed freshwater salmonids, including *S. salar* (Ellis et al. 1985; Lom and Dykova 1992; Hedrick et al. 1993), is caused by an unidentified myxozoan usually referred to as "PKX." This pathogen has, in retrospect, been known for 75 years but was only recognized in the 1980s. The similarity between the observed sporogonic stages of PKX and corresponding stages in *Sphaerospora* species has been stressed and various *Sphaerospora* spp. infecting teleosts such as sticklebacks (Feist 1988; Lom and Dykova 1992) have been identified with the causative agent of PKD. Although Kent et al. (1993, 1994) implicated *Sphaerospora oncorhynchi*, a parasite of mature sockeye salmon in northwest North America, as the PKX organism, Marin de Mateo et al. (1996) have cautioned against accepting this hypothesis uncritically and the most recent molecular study (Kent et al. 1998) has suggested that PKX is not closely related to *Sphaerospora*.

The complex life cycle of myxozoans, which may involve a tubificid intermediate host, makes them unlikely to sustain persistent disease epidemics in the wild although infections from farmed to wild fishes may be possible. The epidemiology of marine myxozoans such as *Kudoa* (Harrell and Scott 1985; Whitaker and Kent 1991) and *Chloromyxum* (Wootten and Smith 1980; Holst et al. 1993; Bristow et al. 1996) species is so poorly understood that their effect on salmon survival or fitness is entirely unknown.

4.3.2. Other protoctistans

A range of protoctistans infect the outer surface of juvenile salmonids. *Ichthyophthirius multifiliis*, a highly pathogenic ciliate, causes greater economic losses worldwide than any other freshwater fish parasite (Cross 1994). This parasite has been recorded from salmon in freshwater hatcheries (Hare and Frantsi 1974; Wootten and Smith 1980; Valtonen and Keränen 1981), where its importance cannot be doubted; its role in wild salmon (Margolis and Arthur 1979) populations is less clear.

The other ciliophorans (e.g., *Capriniana, Chilodonella, Epistylis, Scyphidia, Trichodina*, and *Trichophrya*) are surface-dwelling opportunists, which are ubiquitous in freshwater and may form important components of the skin-surface community. Some may be pathogenic and trichodinids have been associated with the death of kelts (Khan 1991). The mastigophoran, *Ichthyobodo necator*, has a similar ecology (Roubal et al. 1994; Roubal and Bullock 1994) and is well known as a source of mortality in hatcheries. The role of these organisms in juvenile salmonid populations is unknown, but pathogenicity probably depends on unknown factors controlling the precise composition of the ectoparasitic community (Pickering and Richards 1980).

Flagellate species of the genus *Hexamita* cause significant disease problems in a range of fish species, including salmonids (Kent et al. 1992), and under subarctic conditions in Northern Norway a related flagellate, *Spironucleus barkhanus* (see Poppe et al. 1992; Poppe and Mo 1993; Sterud et al. 1997; Sterud 1998), has caused losses among net pen reared salmon. This eurythermic species was originally described from wild grayling (*Thymallus thymallus*) from freshwater river systems in southeastern Norway (Sterud 1998). Other strains infect anadromous Arctic char (*Salvelinus alpinus*) asymptomatically. Infection of Atlantic salmon is believed to have occurred either as juveniles in freshwater or through transmission in the sea from Arctic char. Uneaten surplus food often attracts wild fishes to fish farms, increasing the probability of disease transfer between the wild and farmed fishes (Sterud et al. 1998). Spironucleosis has not been reported since 1992 (Sterud et al. 1998) and there is a general lack of knowledge of the factors triggering spironucleid and hexamitid epidemics.

Other unusual protoctistans occur in aquaculture, for example *Paramoeba* sp., attached to the gills of farmed salmon in Tasmania (Roubal et al. 1989). Such infections are probably due to unnatural juxtapositions of pathogen and host when fishes are translocated outside their normal range, rather than being a normal feature of the host biology. Caged marine salmon may similarly be killed by algal blooms (Dahl et al. 1982; Jones et al. 1982; Bruno et al. 1989; Kent et al. 1995). However, although algae could settle on the gills of smolts or adult salmon moving through coastal waters, their high rate of movement probably prevents morbidity and the problem can be viewed as one of captivity.

4.4. Fungi

A range of fungi have been collected from Atlantic salmon but their impact in wild populations is poorly understood and probably small. The best known is the oomycete *Saprolegnia* sp, frequently recorded from adults and kelts, in association with other pathogens (Johnsen 1978; Roberts 1993), although it can initiate primary infections (Bruno and Stamps 1987). This fungus is also well known for its effects on eggs and immature salmonids in culture (Pickering and Willoughby 1982). It may preferentially infect stressed and hence immunosuppressed (see section 7.3) salmonids (Neish 1977). As an egg pathogen, *Saprolegnia* is also generally a secondary opportunist infecting moribund eggs and Austin and Austin (1987) record infections in the presence of pre-existing *Aeromonas salmonicida*.

Several fungi of the genera *Phialophora* and *Exophialia* also infect salmon; however, only *Ichthyophonus hoferi* is a significant pathogen of farmed salmon (McVicar 1977) and has a major impact on marine fish populations (principally herring) in the northwest Atlantic (Sindermann 1970; Møller and Anders 1986). There is no evidence that this fungus has a significant impact on marine salmon stocks, but further investigations on this point would be worthwhile.

5. Metazoan pathogens

5.1. Monogenea

Salmon are infected by one monogenean with the typical life cycle in which eggs are released into the environment to hatch to a swimming larva. This is the gill parasite *Discocotyle sagittata*. Although potentially pathogenic (see Gannicott and Tinsley 1997), there is no evidence that this parasite causes problems to either wild or farmed salmon.

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One monogenean genus, *Gyrodactylus,* has an aberrant life cycle, retaining embryos in utero until fully grown and already containing a developing embryo. This microparasitic life cycle, with very rapid reproduction in situ upon the host, has resulted in some gyrodactylids being serious pathogens. Salmon are infected by several species, including *Gyrodactylus derjavini* (Mo 1993), *G. salmonis, G. colemanensis,* and *G. nerkae* in Canada (Cone and Cusack 1988; Cone et al. 1983, 1988; Malmberg 1993), *G. caledoniensis* in Scotland (Shinn et al. 1995), *G. truttae* in the Czech Republic (Ergens 1983), and *G. masu* in Japan (Ogawa 1986), all of which are nonpathogenic. In the Baltic Basin, salmon are infected by *G. salaris,* which in Finland is nonpathogenic (Bakke et al. 1990; Rintamaki-Kinnunen and Valtonen 1996). In Norway, however, and in some rivers of the Swedish west coast and the Russan White Sea coast, *G. salaris* is a serious pathogen of wild salmon parr and has been blamed for the significant decline in the fishery (Johnsen and Jensen 1991; Mo 1994, but see also Halvorsen and Hartvigsen 1989). Salmon are also infected by a marine gyrodactylid, *Gyrodactyloides bychowskyi* (Mo and Mackenzie 1991; Bristow et al. 1996), which as far as is known, is nonpathogenic.

5.2. Intestinal helminths

These comprise the Digenea and Cestoda (both Platyhelminthes), the Nematoda, and the Acanthocephala. All have complex life cycles involving at least one, and usually several, intermediate hosts which are links in the food web of the salmon (Køie 1993). This complexity, and the need to coordinate with at least two hosts, means low transmission rates (Kennedy 1985); epidemics rarely occur. Because of the short summers at high latitudes, many helminths become entrained to seasonal patterns of infection (Chubb 1977, 1979, 1980, 1982). Although the individual host may carry an impressive burden of large helminths, the impact on the host population remains small (Halvorsen and Andersen 1984). Some helminths do raise concerns for wild salmon populations (Hoole 1994); the tapeworm *Eubothrium crassum* has sublethal effects on the salmon in sea pens (Bristow and Berland 1991a) and is moderately common in wild salmonids (Kennedy 1978; Andersen and Kennedy 1983; Bristow and Berland 1989) and the nematode may also be pathogenic in freshwater (Larsen & Lund 1997) and may infect fry in large numbers (Hare and Burt 1975a, 1975b). These helminth groups are the most species-rich yet to be considered.

5.3. Extraintestinal helminths

Atlantic salmon is also host to species living extraintestinally including exotic marine species such as *Hepatoxylon squali*. The final host of this tapeworm is the shark, the salmon being an intermediate host which must be eaten for completion of the life cycle. Among the nematodes, the air bladder nematode *Cystidicola farionis* may be pathogenic in freshwater (Knudsen and Klemetsen 1994; Chappell and Owen 1969) and *Anisakis* may have public health significance, as infections of humans can result from consumption of under cooked salmon (Berland and Fagerholm 1994). As this pathogen is associated with pelagic existence (Smith and Wootton 1978), this is peculiarly a risk associated with wild salmon caught during or after their sojourn at sea.

Over 40 species of digenean infect salmon and one is suggested to cause an effect upon the hosts' migratory behavior. The adult digenean *Phyllodistomum umblae* in the ureters of Arctic char and other salmonids may suppress anadromous migration (Nordeng 1983), although this hypothesis has been criticized by Bakke and Bailey (1987). One important digenean group in freshwater, are the eye flukes in the genera *Diplostomum* and *Tylodelphus*. The metacercariae stages of these flukes may blind the infected fish, making it vulnerable to predation, and are important in trout farms (Chappell et al., 1994). They are also important in natural non-salmonid populations (Lester 1977; Kennedy 1981), and, where especially bird predation is a problem they might be expected to have significant effects upon salmon parr survival.

5.4 Crustacea

Sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) represent one of the greatest threats to the salmon marine ranching industry, with the possibility that they may become major pathogens of wild salmonids also. Although known to be occasionally pathogenic (White 1940), sea lice have generally been regarded as relatively harmless in wild populations. However, their importance within sea pens has been increasing since the mid-1960s (Pike 1989), while reports of disease outbreaks in wild salmonids have also increased (Johnson et al. 1996; Grimnes et al. 1996; Tully et al. 1993; Birkeland 1996). Sea lice are epithelial browsers (Boxshall 1974; Pike 1989) and do little damage to this constantly renewed tissue in light infections. Within sea pens however, heavy infections build up, with significant erosion of the epidermis, especially around the head (Jonsdottir et al. 1992). Death then follows, from osmotic shock or secondary infections. In heavy infections of wild fishes, death results from the same epidermal erosion (Grimnes et al. 1996; Tully et al. 1993) and both Calderwood (1905) and White (1940) noted the white head of infected fishes, as skin sloughs off leaving unpigmented tissue. In wild fishes the disease is associated with delays within river mouths (Calderwood 1905; White 1940; Johnson et al. 1996), waiting for water levels to rise, and there seems little doubt that sea louse transmission takes place most efficiently in warm shallow coastal waters (Johnson et al. 1996), although these parasites also survive in the open sea (Nagasawa et al. 1993). It is particularly unfortunate, therefore, that the estuarine environment is also that used for salmon ranching, with release of enormous numbers of sea louse larvae into the environment. Tully and Whelan (1993) recorded naupliar populations of up to 40 million in some Irish embayments and Costelloe et al. (1996, 1998) noted significant densities of nauplii (up to 5 m^{-3}) downstream of salmon farms.

It remains controversial whether sea lice from farmed salmon have a significant effect on wild salmonid populations. In Ireland, the decline in sea trout (*Salmo trutta*) populations from 1989 has been attributed to sea lice and is associated with early return to freshwater of post-smolts (Tully et al. 1993). Although the death of individual wild sea trout due to salmon lice cannot be doubted, the overall impact of this parasite and its involvement in the stock decline

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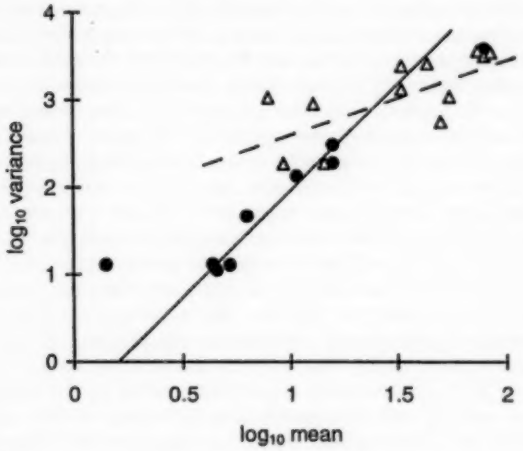
Fig. 4. Taylor's power law applied to recalculated data from Sharp et al. (1994) and Tully et al. (1993) on the occurrence of *Lepeophtheirus salmonis* on Scottish (●) and Irish (Δ) sea trout, respectively. The lower value in Irish fishes suggests that their fish lice populations are less aggregated at high population densities, which indicates an impact on host mortality at the population level. Different population processes are affecting *L. salmonis* in the two areas.



has been questioned (Anonymous 1991; Sharp et al. 1994). In particular, Sharp et al. (1994) argue that the stock decline began before sea louse populations had peaked and that the decline in stocks also occurred in Scotland although sea lice were not a problem. It was noted earlier (section 2) that it was usually difficult to detect significant parasite-induced host mortality at the population level because of the large samples needed. Such samples are available for sea louse infections and it is strange that the methods of Anderson and Gordon (1982) have not been used to resolve the importance of sea lice in the decline of the Irish sea trout fishery. Taylor's Power Law (Taylor 1961; Anderson and Gordon 1982), which predicts a consistent relationship between mean intensity of infection and variance for any given species, shows a different relationship for Scottish and Irish sea trout infected with *Lepeophtheirus salmonis* (data recalculated from Tully et al. 1993 and Sharp et al. 1994). On Scottish fishes, mean intensity of infection is low and the gradient of the relationship between $\log_{10}$ mean and $\log_{10}$ variance is close to 2 (Fig. 4). For Irish fish, however, mean intensity of infection was somewhat higher and the slope of the relationship between $\log_{10}$ mean and $\log_{10}$ variance was close to 1. This lower value in Irish fishes suggests that their *L. salmonis* populations are less aggregated at high population densities. Anderson and Gordon (1982) list parasite mortality, density-dependent processes (e.g., reductions in parasite fecundity), and parasite-induced host mortality as reducing aggregation. The relatively low aggregation of *L. salmonis* on Irish sea trout may therefore suggest an impact on host mortality at the population level and it is clear that different population processes are affecting this parasite in the two areas. While Sharp et al. (1994) are justified in their claim that sea lice do not affect host mortality in Scotland, there can be no justification for the claim that similar processes are at work in Ireland. The relatively low correlation between log mean and log variance in Tully et al.'s (1993) data suggests that a number of disparate processes are occurring in different sampling sites and that further analysis should be undertaken. In particular, it would be interesting to analyze changes in variance:mean ratio within a single cohort through time (Anderson and Gordon 1982) as a sensitive indicator of parasite-induced host mortality. No comparable studies for sea lice on wild salmon exist, although Berland (1993) noted a sharp rise in infection levels between 1988 and 1992. Many published accounts provide only the range of parasite burdens encountered; this limits their value, as no objective measure of the distribution of parasites within the host population can be gained without estimates of both mean and variance. Another problem concerns methods of sampling. If sea lice do influence returning behavior, then sampling regime becomes critical. This has been shown to be the case for sea trout in Norway, where the prematurely returning post-smolts carry significantly larger infections than older migrants (Birkeland 1996). The work of Sharp et al. (1994), however, grouped both pre-smolts and older fishes within the same samples, while Tully et al. (1993) concentrated on pre-smolts. Most studies concentrate on returning fishes and sea trout are likely to be predisposed to sea louse mortalities because they do not migrate far off shore. For salmon the most interesting age group to study, where mortality is most likely to be significant, is the group of smolts passing out through the estuary and not returning. These are a much more difficult group of fishes to sample and as yet no accounts of their sea louse infections have been published.

6. The immune system

6.1. Salmonid immune system

Salmonids have the same sophisticated inducible immune system of other vertebrates (Woo 1992), producing antibodies (Wilson and Warr 1992; Secombes 1994) and having a well developed cellular response (Secombes and Fletcher 1992; Secombes 1994). Nonspecific, humoral responses, including complement, lysozyme, and nonspecific haemolysins (Alexander and Ingram 1992; Sakai 1992) are also well developed and may be a particularly important (Sakai 1992) first line of defense for wild fishes, especially when low temperatures delay antibody synthesis. The complement system may be activated via specific antibodies (the classical pathway) or, in early infections, via complex carbohydrates on the pathogen surface (the alternative pathway). The latter, being antibody independent, can initiate defenses immediately upon invasion. Complement is involved in determining the susceptibility of brook trout to the blood pathogen, *Cryptobia salmositica* (Forward and Woo 1996), and we have found *G. salaris* highly susceptible to salmon complement via the alternative pathway (Harris et al. 1998). Furthermore, variation in serum complement activity has been shown to be a useful marker of disease resistance in selective breeding programmes (Røed et al.1992; Hollebecq et al. 1995).

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6.2. Age and the immune response

The immune system of newly hatched fry matures rapidly over the first few months of life (Ellis 1977; Manning and Mughal 1985; Tatner 1986; Zapata et al. 1997). It is not clear whether alevins can mount a specific immune response; parr can certainly do so and are routinely immunized against a variety of pathogens in aquaculture (Lillehaug 1997). Smolts (Maule et al. 1987; Muona and Soivio 1992) and spawning adults and kelts (Pickering and Christie 1980, 1981; Pickering 1989) may be immunosuppressed as a result of hormonal changes. Precocious dwarf males may also be immunosuppressed and may therefore be important carriers of disease.

The response to different pathogens may vary throughout life. Furunculosis, for example, although still dangerous, appears much less pathogenic to parr and smolt than to adult fishes (Austin and Austin 1987). An additional protective effect is due to herd immunity in very young fishes. An infectious disease introduced into an alevin population may kill many fishes and induce immunity in the remainder but many fishes will also die of unrelated causes and the reproductive output of the pathogen will be limited because of the poor life expectancy of the host (section 3.2). If the same pathogen is introduced into a parr population, on the other hand, the reproductive output will be much greater because of the longer life span of the host. This may have exacerbated the *G. salaris* epidemic in Norway where the response to large-scale parr mortality was to restock with naive parr.

6.3. Stress and disease

Stress raises blood cortisol concentrations (Pickering 1987; Barton and Iwama 1991), reducing immunocompetence and predisposing salmonids to disease (Pickering and Duston 1983; Pickering 1989; Pickering and Pottinger 1989). Sex hormones can also immunosuppress (Pickering and Christie 1980). Stress may therefore immunosuppress asymptomatic carrier hosts, allowing pathogens to multiply and kill the host (Sindermann 1983). The source of this stress is unimportant. Poorly fed fishes are also immunosuppressed (Blazer 1992) and fishes which are low in the dominance hierarchy are likely to be more susceptible to disease. Stock supplementation may therefore not substantially increase the number of smolts migrating to sea, but may provide stressed parr to act as a reservoir of infection and a potential focus for epidemic disease. It is noticeable that UDN (Roberts 1993), furunculosis (Lund 1967), and *G. salaris* (Halvorsen and Hartvigsen 1989) have all been most important when natural stock densities have been very high. Although density dependence in regulation of population size in juvenile salmonids is well documented (Elliott 1989*a*, 1989*b*, 1994), the role of epidemic and endemic disease in generating this phenomenon has not been investigated.

7. The influence of man

Within Europe, little of the range of the Atlantic salmon remains unmodified by man. Salmon have disappeared from much of their historical range and in many rivers can only breed with human intervention. Many populations are exposed to pollution or low and managed water flows. The influence of these factors on parasites and pathogens is particularly difficult to predict. In general, practices such as damming, by slowing river flow and allowing the development of shallow water habitats with emergent macrophytes, would increase habitat stability and complexity, allowing colonization by a wider range of invertebrates, which can act as intermediate hosts for parasites. Eutrophication may simplify invertebrate communities, reducing the range of potential intermediate hosts but also favoring organisms such as *Asellus* and tubificid oligochaetes, which may be important intermediate hosts (Khan and Thulin 1991). Periodic catastrophes, including drought–spate, episodic acidification, or even the deliberate rotenone treatment of rivers to eliminate *G. salaris*, probably have significant, but poorly studied effects on the salmon parasite fauna. A loss of parasites, particularly those with complex life cycles and fastidious ecological requirements, might be predicted. However, reductions in predatory invertebrates could increase the probability of survival of infective parasite larvae, while too little is known of the immunological and competitive interactions between parasites to predict the consequences for the salmonid population of eliminating a single species from the parasite community. The experiences of using rotenone to control *G. salaris* in Norway are instructive in this regard. The parasite was eliminated from fish farms in the early 1990s but continues to persist in many rivers. Episodic rotenone treatment has been employed to eradicate all salmon and hence *G. salaris* from individual rivers. All aerobically respiring invertebrates (most of the insect larvae) are also eliminated, along with all other fishes in addition to the salmonids. Salmonids then recolonize from the sea and by restocking, while invertebrates recolonize by drift from untreated upstream sources. Although recolonization occurs quickly, *G. salaris* has either not been exterminated or has recolonized very quickly three rotenone treated rivers. As far as the authors are aware no environmental impact assessments of the rotenone treatment have ever been published and data are not available to confirm the assertion that the post-rotenone invertebrate fauna is indistinguishable from that before treatment. The range of parasites infecting salmon parr before and after rotenone treatment has also not been compared.

A final nonspecific effect is the slow rise in river temperatures following global warming (Dobson and Carper 1992). Again, the effects on parasite fauna and disease of wild salmonids are impossible to predict. However, low environmental temperatures are immunosuppressive for ectothermic vertebrates, such as teleosts (Bly and Clem 1992), and higher temperatures may lead to enhanced immune responses but thermal stress and low water levels may immunosuppress (see section 7.3). The age at smoltification may be reduced, leading to changes in the age structure of salmonid populations, which will impact upon their disease profile but the longer transmission period may increase disease. It is too early to speculate on the consequences of these changes on salmon parasites; however, we must consider wild salmon as a highly managed resource throughout most of its range and consideration of patterns of disease should form part of the management strategy employed to conserve these stocks.

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7.1. Pollution, stress, and the immune response

In recent years, interest in the interactions between the immune system, disease resistance, pollution, and stress has intensified (Ellis 1981; Bly et al. 1997). The pollution response is largely only a specific case of stress-induced immunosuppression (section 7.3). Stress affects wild fishes more than domesticated strains (Woodward and Strange 1987) and fish diseases are more common in polluted environments (Møller 1985). The interactions of parasites with pollutants are complex and sometimes synergistic (Møller 1986). Such interactions have been largely neglected and field studies linking parasites on salmon with river pollution, comparable with Pippy and Hare's (1969) microbiological investigations, are lacking.

Specific effects of pollutants do also occur. The organophosphates dichlorvos and trichlorfon, widely used in sea louse control, have adverse effects on immune function (Dunier and Siwicki 1993). In general, however, these specific effects remain secondary to the overall immunosuppression induced by the pollutant as a stressor. Similar comments would apply to the observed effects of polychlorinated biphenyls (PCBs) on B-cell function in salmonids (Arkoosh et al. 1994).

In some cases pollution may actually improve fish health when the parasite proves more susceptible than the host. *Gyrodactylus salaris* is particularly sensitive to aluminium in acidified water (Soleng et al. 1996) and this may offset harmful effects of aluminium to the host. Overall, parasites are an important factor in the complex interactions between fish, environment, and man, which can result in disease and mortalities.

7.2. Translocation and introductions of parasites

There is a clear link between introductions and disease, although few introduced pathogens are economically or ecologically important (Kennedy 1994). Two barriers naturally restrict the interchange of salmon parasites in the wild, the osmoti–physiological stress of the fresh-salt-freshwater migration and the homing response which returns spawning salmon to their natal river. These have been highly effective in restricting the dispersal of salmon parasites but have however been broken down by man's movements of salmon stocks (Hoffman 1970; Bauer and Hoffman 1975; Hudson and Hill 1993; Holcik 1991). Translocations have been significant at a number of levels. Locally, the movements of fishes between watersheds by anglers have been significant. In Norway, the watershed of west-flowing rivers inhabited by Atlantic race salmon is separated in some areas by only a few kilometres from watersheds of easterly flowing rivers inhabited by Baltic race salmon and there are fears that *G. salaris* could be spread between these rivers by anglers during the course of a day's fishing (Halvorsen and Hartvigsen 1989; Mo 1994). Additionally, farmed rainbow trout infected with *G. salaris* (which is nonpathogenic to this salmonid, see Bakke et al. 1991) in northern Finland (where *G. salaris* is not a problem) occur only a few kilometres from Norwegian rivers where the introduction of this pathogen into natural salmon populations would be disastrous.

A second level at which translocations take place is with escapees from farms. Estimations of escapes from Norwegian salmon farms run into millions and these fishes, which are less faithful to their natal river and enter later than wild salmon (Økland et al. 1991; Heggberget et al. 1993), are thought to have contributed significantly to the spread of furunculosis (Johnsen and Jensen 1994).

The third, potentially most significant risk of pathogen dispersal has been with large-scale movements of salmonids as part of the international trade in these organisms. This began during the 19th century, with large-scale shipments of salmonid juveniles in both directions across the Atlantic and within Europe. The original epidemic spread of furunculosis in both Europe and America at this time and particularly in the British Isles (Lund 1967) is strongly suggestive of an introduced pathogen. Furunculosis was reintroduced into Norway in this way (Egidius 1987). It should be noted that far fewer risks are associated with the transfer of ova (see section 3.2), which are the preferred form of transfer in modern aquaculture.

There is a very real danger that conservation and stock management arguments for exclusion of infectious diseases can lose out to the political and economic case for free world trade in salmonids and salmonid products. The complexity of this issue is perfectly illustrated by *G. salaris*. There is a ban on the export of live salmon from Norway to prevent dissemination. However, the parasite is not pathogenic in Finland, where it predominantly infects rainbow trout. This fish can be moved within the European Community and *G. salaris* has consequently been introduced into the White Sea coast of Russia from Finland (Mo 1994) and has been recorded from rainbow trout in Germany, Spain, Denmark, and Portugal (Malmberg 1993). These latter countries have no trade in salmon or reason to be especially vigilant against *G. salaris* but every reason to oppose attempts to restrict trade in rainbow trout. The introduction of *G. salaris* into Spain is worrying, given the small number of ecologically sensitive Atlantic salmon populations in that country and the presence of *G. salaris* in all German rainbow trout farms (Lux 1990) may have implications for attempts to reintroduce salmon into the Rhine. Despite vigilance, *G. salaris* will almost certainly eventually invade the U.K., probably with rainbow trout imported from a country far distant from Scandinavia. Fortunately, most parasite introductions fail (Kennedy 1994) and spectacular examples like furunculosis and *G. salaris* are rare.

The final concern is the potential for genetic interchange in parasites from previously isolated host populations. This has been clearly demonstrated in the case of plasmid exchange between *Vibrio* and *Aeromonas* species and could have major effects for genetic change in these organisms. Introduced fish may also form a highly susceptible resource for the multiplication of native parasites normally found on other fishes. For example, brown trout are relatively resistant to the monogenean *Discocotyle sagittata*. Introduction of susceptible rainbow trout to the Isle of Man has led to the development of much larger parasite populations among which genetic exchange can occur freely, with the potential to generate more pathogenic strains (Gannicott and Tinsley 1997).

7.3. Selective breeding and disease resistance

Selection of commercial stocks is generally based on high growth rate and late maturation, little attention being paid to

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disease resistance. Selective breeding for disease resistance (furunculosis and ISA) has been incorporated into the Norwegian breeding programme for salmon only since the early 1990s (Fjalestad 1994) but has identified a genetic component to resistance to *Vibrio* species, BKD and IPN (T. Refsti, Institute of Aquaculture Research, Sunndalsøra, personal communication). Genetic variation in susceptibility to *Gyrodactylus* is also well known (Madhavi and Anderson 1985; Bakke et al. 1990; Leberg and Vriejenhoek 1994; personal observations). The evidence that hosts are heterogeneous in their capacity to develop and express protective responses and that this variation is genetically determined and therefore subject to evolutionary change has important implications concerning epidemiology and as a basis for the development of predictive models for practical disease control (Wakelin 1994). Because fishes with an inappropriate spectrum of disease responses will be rapidly eliminated from the population (see section 2.1), natural populations are optimally selected for resistance to the particular pathogens encountered in their environment. This results in particular allele frequencies for major histocompatibility complex (MHC) polymorphisms, conferring resistance to specific pathogens (Kronenburg et al. 1994). Reintroduction of parr into rivers usually involves fishes, which, while they may be of the same overall genetic background as their parents, have not been selected for disease resistance and their MHC alleles are not normally tested (Dixon et al. 1995). These introductions are usually to replace fishes lost to *G. salaris* or to rotenone treatment (Mo 1994) and may significantly alter the spectrum of MHC alleles present in the natural population. If no account is taken of MHC diversity when restocking, then at best the onset of evolved disease resistance in the managed population could be delayed, while at worst the disease problem could be greatly exacerbated. Similar considerations must apply to escapees and if the scale of escapes is as reported (Johnsen and Jensen 1994) then dilution of resistant MHC genotypes (especially if genetic drift in small breeding populations occurs) may be a major problem. Probes for salmon MHC genes are available (Grimholdt et al. 1993) and it would be of great interest to compare MHC diversity in salmon populations exposed to different patterns of disease, restocking, and interbreeding with escapees.

7.4. Management of wild populations

Stresses due to handling or transport elevate blood cortisol (Pickering 1987), predisposing fishes to disease (section 7.3). Restocking may also influence the establishment of the dominance hierarchy (Kalleberg 1958; Symons 1971), which could in turn modify disease patterns. Restocking programmes may therefore end as experiments in pathogen culture. The addition of smolts, rather than parr, has the additional disadvantage that exposure to pathogens at the start of the life cycle does not occur, preventing the development of immunity, which may be needed later in life.

7.5. Salmon farming and disease patterns in wild populations

Salmonid farms can have profound effects on the abundance of parasite dispersal stages around them. Poynton (1986) found that *Hexamita* were much more abundant downstream of farm outflows than upstream, with associated risks for the wild and managed salmonids of the river. Marine pens in fjords have the greatest potential for this interchange of parasites and pathogens with wild fishes, because they span the migration routes of fishes into and out of the freshwater environment. The complexities surrounding this problem are highlighted by Costelloe et al. (1998), mapping the distribution of sea louse larvae within an estuary utilized by wild salmonids. In this case, high larval densities downstream of the salmon farm could be clearly demonstrated, but other high densities of larvae also existed within the estuary, up to 10 km from the farm. These "hot spots" of larval distribution were probably not derived from farmed fishes but from heavily infected salmonids returning to the river to breed (Costelloe et al. 1998). The relative importance for wild fish of larvae from farmed fish will clearly depend greatly upon the particular hydrographic regime of the river concerned.

Marine pens also have other deleterious effects favoring disease outbreaks. The buildup of waste material (Ackefors and Enell 1994) can lead to sediment enrichment (Johnsen et al.1993) and anoxia (Black et al. 1996), possibly leading to changes in the underlying invertebrate communities. In particular, sediment enrichment and anoxia promote colonization by tubificid worms (Gray 1979; Brinkhurst 1982), which are now known to be intermediate hosts for myxozoans. The high density of farmed salmon in sea cages greatly increases the risk of traumatic skin injury and the spread of pathogens such as fish lice, *Trichodina* sp., *Ichthyobodo*, and *Spironucleus,* which may possibly disperse to passing wild fishes (Sterud et al. 1998). The exchange of plasmids by bacteria in the environment under marine pens has been mentioned previously (section 4.2.1) but should now become less of a problem as antibiotic use is reduced. In all cases, the concern should mainly be for the effect of pathogens from marine pens on smolts passing through the environment, since these fish live for several years and cannot be tracked adequately in the sea.

8. Important future pathogens

The epidemiology of salmonid diseases is still in its infancy. New pathogens are still being discovered and we speculate here on the groups most likely to cause problems in the future and those which may be particularly important for wild and managed salmon stocks.

Gyrodactylus salaris remains a significant concern for eastern Atlantic salmon stocks, particularly the possibility that it may be introduced to the U.K., Ireland, or Iceland. Population models (Clers 1993) suggest an effect on salmon population dynamics, a prediction borne out by Norwegian fishery statistics (Johnsen and Jensen 1988), although other parasites, particularly furunculosis (Johnsen and Jensen 1994), may complicate the Norwegian situation. Much remains enigmatic about *G. salaris*, in particular its patchy distribution as a pathogen (Johnsen and Jensen 1992), interspersed with rivers in which it is less pathogenic (Appleby 1996; Jansen 1994). The discovery of pathogenic populations in the Swedish west coast, where there is no history of introduction (Malmberg and Malmberg 1993), susceptible Baltic stocks (Bakke et al. unpublished data), and relatively resistant Norwegian stocks (Jansen and Bakke 1993*a*;

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Appleby 1996) has confused the original suggestion that *G. salaris* was introduced to Norway recently (cf. Halvorsen and Hartvigsen 1989). Careful modeling studies are needed to assess the epidemiological constraints on pathogenicity in *G. salaris*, preferably integrating the considerable data on gyrodactylid epidemiology (Scott and Anderson 1984; Jansen 1994; Appleby 1996) with a sophisticated model of salmon population behavior.

A further group of pathogens that should be considered are the myxozoans. These parasites are easily disseminated before their pathogenicity has been noticed and eutrophication under salmon pens (Johnsen et al. 1993; Black et al. 1996) could favor their tubificid intermediate hosts (Gray 1979; Brinkhurst 1982). The emergence of PKX, and more recently of the unidentified myxozoan reported by Frasca et al. (1998), indicates the potential of myxozoans as disease organisms and with so little known of the life cycles of marine species their effects upon the survival and fitness of marine phase salmon should be investigated.

Finally we would stress again the position of marine rearing pens as pathogen culture facilities at the crossroads for migrating salmonids moving between fresh and saltwater. We know nothing of the epidemiology of disease of marine salmon, beyond the fact that highly pathogenic organisms such as ISA are unlikely to have a wide distribution in nature because they would kill salmon before they had dispersed. The possibility of organisms such as this colonizing smolts on migration and then having a significant impact on marine salmon stocks should be treated very seriously.

9. Conclusions

Preparing this review has made it very clear that the study of disease in wild salmon populations is in its infancy. In particular, while veterinary viewpoints are well represented in the literature, an ecological focus on salmonid disease is almost entirely lacking. Only two papers, both theoretical, deal with the demographic consequences of disease for salmonids: that of Clers (1993), exploring the potential impact of *G. salaris* on wild salmon, and the work of Levy and Wood (1992), who inferred the existence of a pathogen within pacific salmon populations from the observed population cycles. Detailed field observations, comparable to those of Costelloe and coworkers (Costelloe et al. 1996, 1998) on the dispersal of infective sea lice larvae within and between host metapopulations, are almost entirely lacking for the majority of pathogens, including the important *Gyrodactylus salaris*. Management decisions, for example restocking after depletion of a natural population by *G. salaris*, are not being informed by consideration of their likely epidemiological consequences, although an adequate theoretical framework for this has been published (Anderson 1982). There is a need for integration of general epidemiological theory (Anderson 1982; Grenfell and Dobson 1995; Swinton et al. 1998) into the sphere of salmonid biology and management. At the same time, much more research into the diseases of wild salmonid populations, not only during conspicuous and costly epidemics, is desirable. We are particularly lacking in data on the role of disease in early life cycle stages (fry and parr) and on events during the marine phase and positive efforts must be made to target these life cycle stages rather than the well-studied and demographically less important adult returners. Apart from field studies of the role of disease in natural salmon populations, there should also be attempts to integrate the findings of such studies into quantitative models of salmon population behavior (e.g., that of Korman et al. 1994) to gain an insight into the possible role of pathogens and parasites in controlling salmonid abundance and growth. Given the very large number of salmon pathogens and parasites known and given that spectacular epidemic diseases (e.g., furunculosis) occur, it is almost inconceivable that endemic disease does not play a part in salmon ecology. Our success in managing, conserving, and ultimately reintroducing Atlantic salmon throughout its former range will ultimately depend in large part on our success in understanding these disease processes.

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Spatial variation in environmental characteristics of Atlantic salmon (*Salmo salar*) rivers

Scott R. Elliott, Treva A. Coe, James M. Helfield, and Robert J. Naiman

Abstract: Rivers and streams occupied by anadromous Atlantic salmon (*Salmo salar*) occur across a diverse array of landscapes. This article describes the general ecology of these rivers and streams, including many of the physical and biological variables that are important characteristics of all lotic systems. For analytical purposes, the geographic range of Atlantic salmon rivers is divided into five regions, based on geomorphology and climate. The physical habitat available to anadromous Atlantic salmon is diverse. The geology varies from granitic bedrock to volcanic and glacial substrates, which influence a broad array of other ecological variables, ranging from water chemistry to catchment morphology (e.g., river length). Flood regimes and system hydrology are dependent, as expected, on climate. Many of the catchments receive substantial precipitation in the form of snow; rivers in four of the five regions experience primarily spring freshets. Aquatic temperatures are also variable, representing close to the full range of thermal tolerance of *S. salar*, with lows just above 0°C in the northernmost latitudes to summer highs in western Europe approaching 25°C. Most rivers are best characterized as oligotrophic with relatively low annual primary productivity. However, physical factors such as availability of suitable spawning and rearing habitat, as well as aquatic temperature and flow regimes, may drive anadromous productivity. In general, most of the rivers have been modified by flow regulation and many suffer from impacts related to other anthropogenic disturbances, principally riparian forest clearing for agriculture, forestry, and urban development. We conclude that the rivers and streams occupied by anadromous Atlantic salmon are diverse across the species' range and have been heavily impacted by anthropogenic disturbances.

Résumé : On trouve les cours d'eau fréquentés par le saumon de l'Atlantique anadrome (*Salmo salar*) dans divers types de paysages. Le présent article décrit l'écologie générale de ces cours d'eau, dont bon nombre des variables physiques et biologiques qui sont d'importantes caractéristiques de tous les milieux lotiques. Aux fins de l'analyse, l'aire géographique dans laquelle on trouve les rivières à saumon est divisée en cinq régions sur la base de la géomorphologie et du climat. Le saumon atlantique anadrome fréquente des habitats physiques divers. Sur le plan géologique, on trouve aussi bien des substrats granitiques que des substrats volcaniques ou glaciaires, lesquels déterminent une vaste gamme d'autres variables écologiques, comme la chimie de l'eau et la morphologie du bassin versant (p. ex., la longueur des cours d'eau). Les régimes de crue et l'hydrologie des bassins dépendent, comme on peut s'y attendre, du climat. Bon nombre de bassins versants reçoivent une part substantielle de précipitation sous forme de neige; les cours d'eau de quatre des cinq régions connaissent principalement des crues nivales. Les températures de l'eau sont aussi variables : elles couvrent presque entièrement la plage de tolérance thermique de *S. salar*, avec des minimums juste supérieurs à 0°C sous les latitudes septentrionales et des maximums estivaux approchant 25°C en Europe de l'Ouest. La plupart des cours d'eau sont oligotrophes et montrent une productivité primaire annuelle relativement faible. Cependant, des facteurs physiques comme la présence d'habitats favorables pour la reproduction et l'alevinage, de même que la température de l'eau et les régimes d'écoulement, peuvent encourager la productivité du saumon anadrome. En général, la plupart des cours d'eau ont été modifiés par la régulation de leur débit, et bon nombre ont subi des impacts négatifs liés à d'autres perturbations anthropiques, principalement à la coupe des arbres sur leurs rives pour l'agriculture, l'exploitation forestière ou le développement urbain. Nous concluons que les cours d'eau fréquentés par le saumon atlantique anadrome montrent une grande diversité d'un endroit à l'autre de l'aire de répartition de ce poisson et ont été fortement perturbés par les activités humaines.

[Traduit par la Rédaction]

"And the star-stream of heaven flowed westward, to far beyond the ocean where salmon, moving from the deep water to the shallows of the islands, leapt — eager for immortality.

Henry Williamson (1935), excerpted from *Salar the Salmon*

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S.R. Elliott[1] and J.M. Helfield. College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98195, U.S.A.
T.A. Coe and R.J. Naiman. School of Fisheries, Box 357980, University of Washington, Seattle, WA 98195, U.S.A.

[1]Author to whom all correspondence should be addressed. e-mail: elliott@u.washington.edu

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Introduction

The basic concept of rivers as a continuous series of integrating physical gradients and associated biotic adjustments has provided the holistic perspective needed for discovering and understanding how variations in the physical environment are ecologically relevant to widely distributed species (Vannote et al. 1980; Naiman et al. 1987). For some time it has been known that the characteristics of running waters reflect local geomorphology, climate, disturbance regimes, and features of the riparian ecotone (Décamps and Naiman 1989; Naiman and Bilby 1998). As a consequence, individual river segments acquire unique features related to position in the catchment, patterns of water movement, channel gradient, and accessibility to colonizing organisms. The ecological consequences of the physical variability within catchments, as well as between ecoregions, are expressed as variations in life history strategies, evolutionary processes, ecosystem integrity, and patterns of biodiversity. Variations in these ecological characteristics have, in turn, strong implications for management and restoration strategies.

This is especially true in the numerous Atlantic salmon (*Salmo salar*) rivers draining into the North Atlantic Ocean, the Norwegian Sea, and the Barents Sea. Strong gradients and contrasts in parent geology, topography, soils, temperature, and flow regime exist within these rivers, encompassed within 40° to 60° north latitude in North America and from 40° to 70° north latitude in Europe (Netboy 1973). Describing patterns in the physical environment and understanding processes creating and maintaining those patterns provides a fundamental foundation for interpreting trends in Atlantic salmon life histories and productivity and the biotic communities supporting them.

In this article, we investigate the breadth of this heterogeneity by examining the general biophysical characteristics of rivers within the natural range of Atlantic salmon. The objective is to provide an overview of regional patterns in geomorphology, climate, hydrology, water temperature and chemistry, aquatic biodiversity, and productivity, as well as riparian characteristics (Table 1). These patterns are described (in so far as possible) for natural rivers and discussed in light of recent land use changes, with several case studies provided as illustrations. In making connections between biophysical characteristics and salmon ecology and production, we seek to identify factors which may make certain rivers more productive than others and to elucidate differential vulnerability to various anthropogenic stresses. An understanding of these factors is essential to guiding management, conservation, and restoration strategies of salmon-bearing streams.

Regional analysis

The range of *S. salar* historically included every country with rivers draining into the North Atlantic Ocean, the Norwegian Sea, and the Barents Sea. Currently, the range of Atlantic salmon rivers extends from New England through the eastern seaboard of Canada, across to Greenland and Iceland, eastward through Scandinavia to Russia, and south and westward to the British Isles, France, Spain, and Portugal (MacCrimmon and Gots 1979).

For the purpose of analysis, we divided the range of *S. salar* into five major regions (Fig. 1) according to differences in geology, flow regime, and climate, coupled with geographic position (Fig. 2). Although based on catchment variables, the scheme is generally supported by studies which have clustered Atlantic salmon populations according to genetic and other characteristics (Davidson et al. 1989; Table 2).

Region I: New England, Nova Scotia, and Gaspé Peninsula

This region includes the Gaspé Peninsula, New Brunswick, and Nova Scotia in Canada, as well as the northeastern United States. Topography ranges from gentle, rolling granite uplands to areas with much greater relief such as the White Mountains in New Hampshire. The geology of New England is characterized by folded overthrust sediments with metamorphics and igneous intrusives (Strahler 1975). River channels bear evidence of extensive modification during the Pleistocene by glacial scour and deposition. The region has undergone recent glacial modification; glacial deposits overlying bedrock average 8–15 cm but can reach 120 m in some river valleys (Webster et al. 1995). The summer climate is mild (10–20°C) to hot (>20°C) with cool to cold winters (<10°C; National Geographic Society 1992).

Region II: Canadian Shield

The Canadian Shield extends from Labrador and Québec around Hudson Bay to central-eastern Canada (Sutton 1972; Mackay 1995). Underlain by Precambrian deposits, the region is characterized by granite bedrock either exposed or overlain by thin soils (Mackay 1995). Much of the region consists of a flattened plateau (<1000 m elevation) of low or undulating relief dissected by deep valleys with a few mountains penetrating above the plateau (Power 1981). Rivers flowing to the St. Lawrence River cut through the plateau, often resulting in very abrupt changes in elevation with rapids and falls presenting natural barriers to fish passage (Netboy 1980). In Labrador, areas rich in limestone and sandstone deposits also occur (Anderson 1985). Rivers in Labrador either flow over relatively flat topography or through deeply incised valleys to the Labrador Sea. Here the Shield is characterized by numerous areas of standing waters which form lakes, swamps, and bogs (Anderson 1985; Mackay 1995). Mild to cool summers and cold winters typify the climate, with mean daily temperatures ranging from –10 to –25°C in January to 10–15°C in July (Geographical Services Division 1985).

Region III: Northern Islands

The Northern Islands region is comprised of the harsh environments of Iceland and Greenland. The geology of Iceland is heavily influenced by volcanic activity with a plateau of volcanic rock forming the interior of the island (Petersen et al. 1995; Netboy 1980). Recent lava and palagonite formations comprise the interior of the island from the southwest through the central highlands to the northeast coast, with basalt lying to the west and east (Einarsson 1968). The

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Table 1. Selected bophysical characteristics of Atlantic salmon rivers by region.

Region	Geology	River length (km)	Flood regimes	Aquatic temperature regime[a] (°C)	Length of growing season	Role of ice	[DOC] mg C·L^{-1}	Productivity	Diversity	Riparian	Land uses/Major impacts
I	Glacial deposits overlying bedrock	5–552	March, April freshet	ND; 20–25+	150 to 170[b]	Not important	4	Low, variant		Significant hardwood component	Urbanization, agriculture, regulation
II	Exposed granitic bedrock	1–546	April, May freshet	0–0.4; 15–22	80 to 170[b]	Under ice cover from ~Dec. to ~March	10–15	Low, variant		Primarily boreal forest	Forestry
III	Volcanic, some glacial	93–320	Spring freshet	0–5; 3–5+	ND	Spring fed, volcanically–influenced rivers do not freeze over; arctic/alpine rivers will freeze over	?	A *f*(*n*) of arctic light regimes; minimal riparian cover		Low woody shrubs and grasses; little riparian cover	Few
IV	Calcareous or granite/gneiss substrate	94–1809	Winter freshet along coast of Denmark, Atlantic coast of Norway; boreal regions experience Spring freshet	0–5; 11–23	63 to 192[c]	Boreal/alpine streams freeze over; coastal systems remain clear	15–45	Low, variant		Primarily boreal forest	Regulation
V	Glacial deposits; chalk; boulders and rocks (uplands); alluvial in lowlands	19–1110	Winter freshet	0–4; 12–25	196 to >330[c]	Not important	5–7	Low, variant		Mixed forests; significant clearing for agriculture	Urbanization, agriculture, regulation

[a]Minima and maxima ranges, respectively.
[b]Number of days greater than 5.6°C.
[c]Number of days greater than 7.0°C.

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Fig. 1. Natural geographic range of Atlantic salmon rivers.

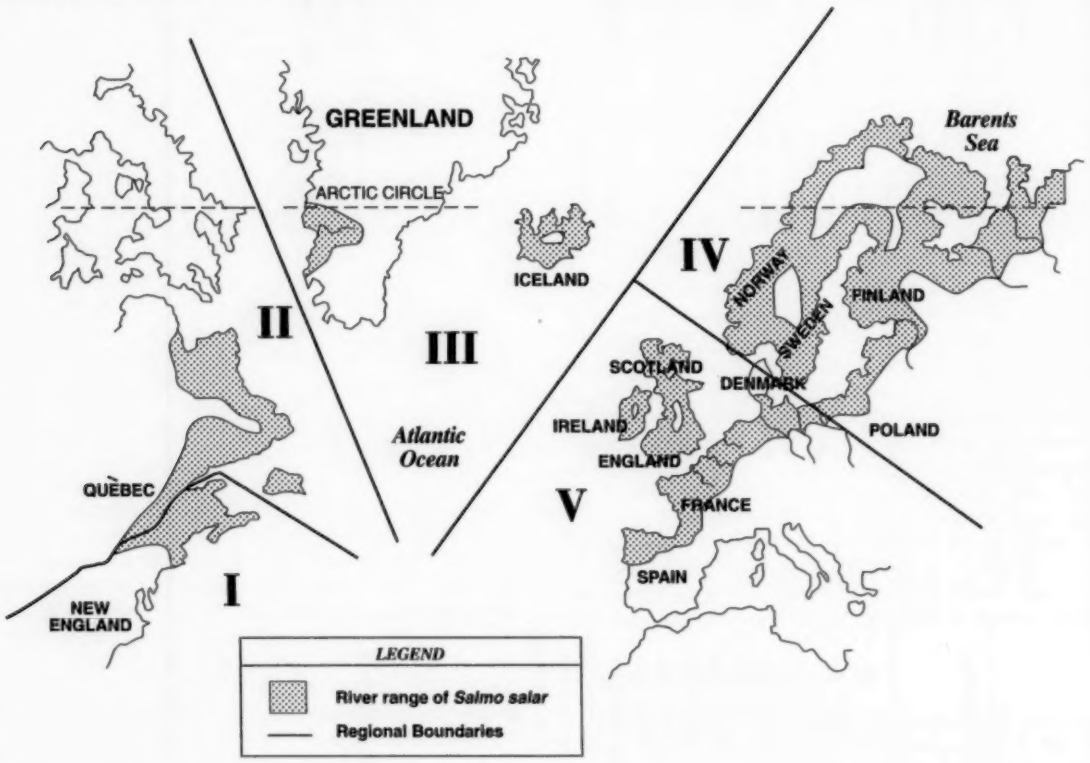
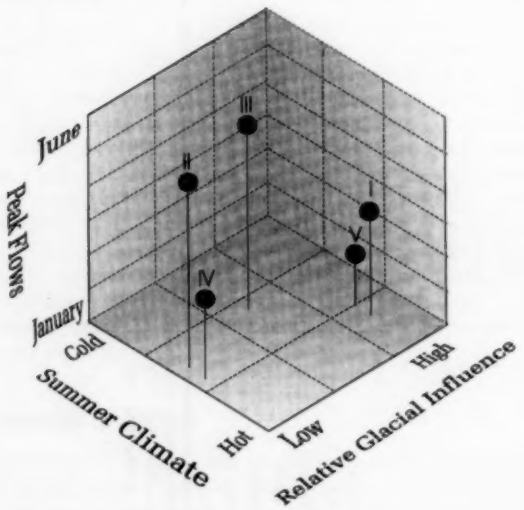


Fig. 2. Clustering of regions according to climate, flow regime, and glacial influence.



numerous rivers tend to be fast and large and are influenced by either glaciation or volcanism. Lakes and areas of standing water are also numerous. Rist (1956) identified four types of Icelandic rivers with different flow and temperature regimes depending on source type: direct runoff, lake or standing water fed, spring fed, and glacier fed. Iceland has a humid and temperate climate (Netboy 1980). Mean monthly air temperature for middle Iceland ranges from –10°C in January to 6°C in July (Petersen et al. 1995). Atlantic salmon spawn in only one river in Greenland, the Kapisillit, on the southwest coast of the island (Shearer 1992).

Region IV: Scandinavia and Russia

Scandinavia includes Denmark, Finland, Norway, Sweden, and Poland. The geology of Scandinavia is of two distinct types: the first, encompassing Denmark and southern Sweden, consists primarily of glacial moraine deposits; the second is composed of Archaean crystalline rocks and dominated by the Fennoscandinavian Shield, a formation sloping gently toward the southeast. Low-gradient rivers in this region flow over calcareous or granite/gneiss substrates with thin soils while high-gradient streams exhibit bare granite geomorphology. Rivers range from low-gradient streams interspersed with lakes, ponds, and wetlands, to high-gradient mountain streams dominated by cascades and waterfalls. Generally, Nordic rivers are short in length and small in catchment area (Petersen et al. 1995). Salmon rivers in Russia are generally longer and drain greater areas (Netboy 1980) than Nordic rivers. The general climate is one of mild (10–20°C) summers and cold (<0°C) winters (National Geographic Society 1992); mean annual air temperature ranges

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Table 2. Genetic and geographic groupings of Atlantic salmon.

Region	Thorpe and Mitchell 1981		Stähl 1987		Møller 1970
I	North American		Canadian		New Brunswick/ Nova Scotia; Maine
II					Newfoundland/ Labrador
III	European	Western	European	Eastern Atlantic	
IV		Northern; Baltic		Baltic	
V		Western		Eastern Atlantic	

Note: Stähl 1987: Inferred from dendrogram constructed from genetic distance matrix based on allele frequencies at 38 loci.
Møller 1970; Mitchell and Thorpe 1981: Based on differences in transferring allele (TF^A) frequencies.

from 8°C in southern Sweden to 2°C in the arctic region (Petersen et al. 1995).

Region V: Western Europe

The European countries of the United Kingdom, Ireland, Belgium, Netherlands, Germany, France, Spain, and Portugal present a wide diversity of Atlantic salmon habitat. Rivers in Britain, for example, are generally small relative to other rivers of the world (Ward 1981). They arise in chalk, sandstone, limestone, or from metamorphic or igneous rock in low elevation mountains and flow at low gradients through clay or alluvium (Ladle and Westlake 1995). Streams in the north and west are typically steep, fast, and rocky with little intervening floodplain while those of the south and east are slower and more meandering with pronounced floodplains (Newson 1981; Ladle and Westlake 1995). The area encompassing France, Belgium, and the Netherlands consists of two large plateaus of secondary and tertiary sedimentary rocks surrounded by three uplift Hercynian massifs (Billen et al. 1995). Rivers in the area tend also to be short with relatively small basins, although there are several major river systems which are substantially larger. The lowlands of this region often have well-developed alluvial plains (Billen et al. 1995). Salmon rivers in Spain and Portugal are confined to the north and northwest portions of the Iberian Peninsula, which receive substantial rainfall distributed somewhat evenly throughout the year. Streams arising in the mountains are short, fast, and cold, flowing through deeply incised valleys with numerous rocky ledges and cascades (Netboy 1980); they tend to be spate rivers, quick to rise and fall (Garcia de Leaniz and Martinez 1988) and drain granite and basalt formations (Sabater et al. 1995). Despite such variety in upland geomorphology, rivers of the western European region have somewhat similar climates. Mild (10–20°C) summers and cool (0–10°C) winters, while Spain and eastern Europe tend towards higher and lower temperatures, respectively (National Geographic Society 1992).

The physical environment

Catchment morphology

Lengths of 70 rivers on the Gaspé Peninsula and in Nova Scotia and New Brunswick (Region I) range from 5 to 343 km ($\bar{x}$ = 59 km; Schaffer and Elson 1975). Combined river length data from Region II (Québec, Newfoundland, and Labrador; n = 17, 47, and 102, respectively; Schaffer and Elson 1975; Anderson 1985) yielded a greater range (1–546 km) but a similar mean of 57 km. Comprehensive data sets such as these apparently are not available for other regions, where lengths for major river systems only were reported; in such cases, it may be more valid to compare upper levels in length ranges. Three of New England's (southern Region I) largest rivers, for example, are 340–552 km long (Unesco 1978), comparable to the upper level for rivers to the north of the region. Petersen et al. (1995) provide lengths for three representative rivers (from Regions III and IV) in each of five countries: Iceland (93–230 km), Denmark (94–146 km), Finland (507–560 km), Norway (302–601 km), and Sweden (450–720 km). Rivers in Russia extend in length from the relatively short rivers of the Kola Peninsula to the broad, slow-flowing Pechora River, the largest of Atlantic salmon rivers at 1809 km (Unesco 1978; Kuz'min and Smirnov 1982). In England (Region V), Atlantic salmon rivers range from 82 to 239 km (Ward 1981) with Scottish rivers substantially shorter (19–158 km, $\bar{x}$ = 26; Thorpe and Mitchell 1981). Salmon rivers in France are longer than in the United Kingdom, from the 650 km Garonne to the 1110 km Loire (Unesco 1978), while those in Spain are shorter, generally <50 km (Garcia de Leaniz and Martinez 1988).

Catchment size, or drainage area, is positively and strongly correlated with river length for all regions considered (Fig. 3). The slope of this relationship reflects patterns in geology and hydrology and might be expected to differ substantially among regions, yet there are no apparent regional patterns other than differences in absolute river and catchment sizes. The three large river systems in New England (southern Region I) drain 29 000 to 35 000 km^2 (Unesco 1978). Drainage areas range from 13 to 93 415 km^2 ($\bar{x}$ = 2225 km^2) for 102 Labrador rivers (Region II) (Anderson 1985). Similar data for river length is presented for drainage areas of Icelandic and Scandinavian rivers (Regions III and IV, respectively; Petersen et al. 1995): Iceland (2000–8000 km^2), Denmark (1000–3000 km^2), Norway (16 000–42 000 km^2), Sweden (32 000–50 000 km^2) and Finland (40 000–62 000 km^2). Values for Region V range from 1090 to 9950 km^2 for 20 Great Britain rivers (Ward 1981) with relatively large values evident for Belgium and France (13 489–120 000 km^2, n = 4; Unesco 1978). Drainage areas for 6 rivers in Asturias, Spain, however, are much smaller, only 467–2572 km^2 (Ventura 1988).

Catchment size has obvious implications for the ecology and life history strategies of Atlantic salmon. Smaller river systems tend to have lower discharges and more variable flow regimes, potentially confining upstream migration to a narrower time frame. Longer rivers are associated with lon-

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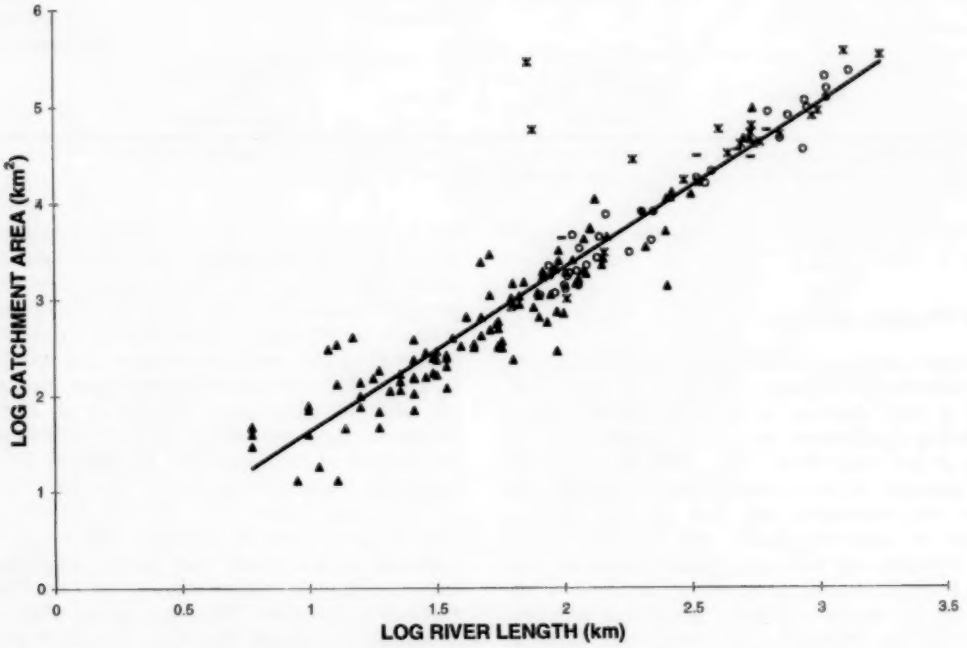
Fig. 3. Relationship between river length and drainage area for Atlantic salmon rivers. Regression equation: $y = 1.6921x - 0.0744$ ($r^2 = 0.8829$). — = Region I ($n = 5$); ▲ = Region II ($n = 105$); ● = Region III ($n = 3$); * = Region IV ($n = 31$); ○ = Region V ($n = 22$).



ger periods at sea and higher mean age of first spawning (Schaffer and Elson 1975), presumably due to the difficulty of upstream migration in such rivers. Difficult migrations in long, fast rivers may also lead to increased postspawning mortality and subsequent reduction in frequency of iteroparity. In any comparison, it is important to consider factors such as barriers to fish passage and availability of suitable habitat lower in the catchment which may reduce the length of river actually used by salmon.

Hydrology

In catchments unimpacted by human activities, hydrology is controlled by climate, precipitation, and geology. Accordingly, Atlantic salmon rivers tend to follow one of two generalized patterns of annual discharge. In cold regions, peak flow timing is determined by the extent to which runoff inputs are delayed in snow and ice. In warmer climates without appreciable snow or ice cover, peak flows are controlled by seasonal changes in rates of precipitation and evapotranspiration. Under these different hydrologic scenarios, different factors affect growth and survival rates of Atlantic salmon.

Where winter precipitation occurs primarily as snow, or where surface waters are frozen for some portion of the winter, discharge volumes are highest during spring melt. For example, an average of 54% of annual streamflow at Hubbard Brook, New Hampshire occurs between March and April (Likens et al. 1977). Similarly, 50% of annual discharge in subarctic Québec streams occurs during April and May freshets, whereas January and February flow volumes represent only 3–5% of annual maxima (Naiman and Link 1997). This pattern of snowmelt-driven peak flows in spring and relatively low flows in winter is evident throughout New England (Region I) and Québec (Region II), as well as in the boreal, arctic, and alpine regions of Iceland and Scandinavia (Regions III and IV, respectively) (Mackay 1995; Petersen et al. 1995; Webster et al. 1995; Naiman and Link 1997).

During winter and early spring, flood magnitudes in these areas are influenced by instream ice formations. Where high flows interact with ice cover at the time of spring breakup, ice jams can deflect flow onto the banks and exacerbate spring flooding (Prowse 1994; Scrimgeour et al. 1994). During winter, anchor ice on the river bed serves to elevate the effective river stage, while ice blockages may lead to rapid increases in water level immediately upstream and decreased flow in downstream reaches (Prowse 1994; Cunjak 1996). Anchor ice or partial ice blockages may also decrease channel cross-sectional area, resulting in localized increases in flow velocity and potentially increased bed scour.

Despite these effects, salmonids in snow and ice-influenced regions are more typically threatened by low flows in winter. During the winter low flow period, physical space is a major factor regulating stream fish populations. As overwintering habitat area decreases, fry may experience high rates of mortality due to stranding and subsequent suffocation, as well as freezing and increased predation pressure (Cunjak 1996). Low winter discharges also reduce percolation of water through redds, resulting in decreased delivery of dissolved oxygen and correspondingly decreased rates of survival for incubating eggs (Chadwick 1982). Moreover, reduced flows may result in lower temperatures

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and egg mortality typically increases at temperatures below 4°C (Peterson et al. 1977). Accordingly, there is a positive correlation between winter discharge and survival of juvenile Atlantic salmon in boreal rivers of Newfoundland and New Brunswick (Gibson and Myers 1988).

Another factor that may affect salmonid reproduction in ice-influenced areas is the potentially limited spawning season. In spring, migrating salmon will not enter the river until after breakup and its associated freshets, yet spawning must occur earlier in fall, before tributaries are closed by ice. For example, few salmon enter the Nepisiguit River in northern New Brunswick (Region I) before late June or early July, and spawning typically ends in late October or early November (Nepisiguit Salmon Association 1995), whereas salmon may enter more temperate British Rivers (Region V) at all seasons of the year (Netboy 1968).

In more temperate, coastal regions, where almost all winter precipitation occurs as rain, seasonal patterns of discharge tend to reflect increased precipitation during winter and increased evapotranspiration in summer. In the coastal, deciduous regions of Denmark and the Atlantic coast of Norway (Region IV), where periods of below-freezing temperatures are relatively short, high flows occur in winter, and low flows occur in late spring through summer (Petersen et al. 1995). Similarly, peak flows in British streams (Region V) occur in winter and low flows occur in summer through early fall (Ward 1981; Ladle and Westlake 1995). In these regions, high winter flows may result in increased scouring of salmonid redds and correspondingly increased mortality of incubating eggs. These effects are exacerbated by rain-on-snow events where periodic snowfall is followed by warm rains, resulting in pulses of snowmelt during winter. Whereas summer discharge appears to be unrelated to survival in boreal rivers (Gibson and Myers 1988), low summer flows and stranding may have significant effects on survival rates for juveniles in these warmer regions of the Atlantic salmon's range. Positive correlations have been reported between summer discharge and survival of underyearling salmonids in coastal rivers of Britain (Elliott 1984; Solomon and Paterson 1980).

Discrepancies between flow maxima and minima are influenced by sources and pathways of water from the landscape to the stream channel, which are in turn influenced by catchment geology and topography. In catchments with high infiltrative capacities, a higher proportion of streamflow will be groundwater fed and annual discharge is more evenly distributed in time. For example, in the calcareous chalk areas of southern and eastern England, infiltration rates are high and up to 90% of discharge can be from groundwater (Paolillo 1969). Maximum:minimum discharge ratios of chalk streams range from 5 to 10, as compared with ratios of 30:300 in northwestern British streams draining more impervious, rocky basins (Ladle and Westlake 1995).

Aquatic temperature regimes

Given the considerable latitudinal gradient in the range of Atlantic salmon, variation in annual temperature ranges among rivers of different regions is not surprising. Two streams in New Brunswick (Region I) showed maximum annual water temperatures in the range of 20–22°C (Riddell and Leggett 1981) while two rivers in Maine, U.S.A., exceeded 25°C for 4–5 d·yr^{-1} (Hulbert 1978). The typically cool winters in Region I suggest temperatures do not normally result in extreme ice conditions. Rivers in Québec and Labrador (Region II), on the other hand, tend to be under extensive ice cover from December through March and are considerably cooler year round (Mackay 1995), as reflected in the mean annual air temperature of only 6°C for the region. Minimum water temperatures are near 0°C while summer maxima range from about 22°C in southern Québec (Naiman et al. 1987) to just 15°C in Ungava Bay, northern Québec (Jensen and Johnsen 1986). Temperatures in Icelandic rivers (Region III) are influenced by source type. Spring-fed rivers in the volcanic zone do not freeze in winter and, moreover, maintain fairly constant temperatures of 3–5°C year round (Rist 1956; Petersen et al. 1995). Those draining high mountain areas, however, are more variable and, due to influence of snowmelt in spring and early summer, remain cold even during the short growing season (Rist 1956). Jensen and Johnsen (1986) list annual ranges of 1–11°C for two rivers in northern Norway (Region IV) and 4–13°C for a river in western Norway, while rivers in central Scandinavia reach maximum temperatures of >14°C (Petersen et al. 1995). The Pechora River in northwestern Russia exhibits considerably higher temperatures than the coldest Norwegian rivers, reaching 23°C in summer (Jensen and Johnsen 1986). The annual temperature range for British rivers (Region V) is 1–20°C; the range varies for different streams in the same region: 0–25°C for low-order streams in general (Walling and Webb 1981), but only 11–12°C for chalk streams (Ladle and Westlake 1995). Belgium's Meuse exhibits a similar range (0–23°C) with mean 7–9°C annually (Descy and Empain 1984) while in Spain, river temperatures fall below 7°C only 1–2 mo·yr^{-1} (Garcia de Leaniz and Martinez 1988).

Growing season also varies considerably among Atlantic salmon rivers although comparison is somewhat confounded by differences in units reported in the literature. When expressed as number of days (d) air temperature exceeds 5.6°C (Power 1981), growing season among Regions I and II is greatest for the tip of Gaspé (150–170 d), followed by insular Newfoundland (120–170 d), southern Québec (120–160 d), and central and northern Québec and Labrador (80–120 d). A similar measure of growing season is the number of days that water temperature exceeds 7°C and is comparable only when river temperatures closely track air temperatures; growing season expressed thus for a New Brunswick river (146 d water temperature > 7°C, Symons 1979) was similar to that given above for Gaspé. Data are unavailable for Region III, although it is expected that the values might be similar to, if not slightly less than, alpine Norway (see below). Growing seasons in Region IV are also influenced by latitudinal effects, with 192 d (water temperature > 7°C) for a Swedish river, 149 d (average; 119–178 d range) for a river in western Norway, and 63 d (averaged; 54–87 d range) for a river in northern Norway (Jensen and Johnsen 1986). Higher growing seasons (expressed in this same form) have been reported for rivers in Region V, with 196, 262, 315, and >330 d for a river in each of Scotland, France, England, and Spain, respectively (Symons 1979; Garcia de Leaniz and Martinez 1988).

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Perhaps a better indicator of growing season, however, is the growth opportunity index (G) which integrates both temperature and daylength with the equation:

$$G = \sum T_i D_i$$

where T_i is mean air temperature >5.5°C and D_i is the hours of daylight in month i (Metcalfe and Thorpe 1990). This index facilitates direct comparison of rivers across latitudes without the need to correct for photoperiod. Indeed, growth opportunity index explained 82.3% of the variance in mean smolt age among 182 rivers throughout the geographical range of Atlantic salmon, whereas latitude alone (a proxy for temperature) accounted for only 6.1% (Metcalfe and Thorpe 1990). The study compared rivers of the eastern Atlantic coast of Canada (Region II; G = 3–23°C·h·10^3; n = 52) to those in western Europe (Regions IV and V; G = 7–39°C·h·10^3; n = 101) and those draining into the Baltic and White Seas (Region IV; G = 10–24°C·h·10^3; n = 29).

Temperature range and length of growing season have obvious implications for salmonids. Low mean temperatures and short growing season result in lowered annual growth rates for rearing juveniles (Jensen and Johnson 1986) and hence higher mean age of smolts (Power 1981). Temperature also influences length of egg incubation period and longer incubation periods in colder rivers may lead to earlier spawning by adult salmon to ensure emergence at optimal times. High summer water temperatures may also approach upper lethal limits for salmon, especially in the southern regions.

The biological environment

Productivity

Most, if not all rivers within the range of Atlantic salmon are best characterized as oligotrophic, with net primary productivity (NPP) data reflecting relatively low annual productivity (Naumann 1932; Ladle and Westlake 1995). A study on the Fort River in Massachusetts yielded an average periphyton NPP of 0.38 g C·m^{-2}·yr^{-1}, with a range of 0.003–0.76 g C·m^{-2}·yr^{-1} (Fisher and Carpenter 1976), while periphyton NPP values calculated on salmon rivers in southern Québec show values ranging from 0.3 to 1.0 g C·m^{-2}·yr^{-1} (Naiman 1983). Data for productivity for Iceland and Greenland (Region III) are not available, but accessible information suggests that algal communities thrive in these harsh lotic systems and that primary production is important (Petersen et al. 1995). Perhaps this is related to this region's minimal riparian cover, as gross primary productivity (GPP) is significantly related to percent canopy cover (Lamberti and Steinman 1997). A study in southeastern Finland (Region IV) indicated low productivity, with values ranging from 0.09 to 0.8 g C·m^{-2}·yr^{-1} (Holopainen et al. 1988). NPP data from the Meuse River basin (Region V) were somewhat analogous to the Massachusetts data (Region I) (Scailteur 1982). Even though these data reflect low annual productivity, some environmental factors (e.g., a seasonally variable photoperiod) may account for high productivity during certain periods of the year. In some of the northernmost areas, for example, productivity may be quite high during the summer months when the photoperiod is extended and average daily water temperatures reach an annual peak. This small "burst" of productivity may be of critical importance to the trophic base supporting juvenile *S. salar*.

In boreal catchments where humic and fulvic materials are leached from peat bogs, DOC concentrations may be as high as 10–45 mg C·L^{-1} (Naiman and Link 1997; Petersen et al. 1995), as opposed to deciduous regions where concentrations are typically <10 mg C·L^{-1} (Webster et al. 1995; Meybeck 1985). Studies of blackwater rivers in the Amazon (e.g., Devol 1984) suggest that primary productivity may be limited by light extinction in these darker, high-DOC waters. Enhanced microbial activity associated with high DOC inputs may also result in increased community respiration in bottom and subsurface sediments (Findlay 1995). Accordingly, salmon eggs incubating in boreal rivers may be at greater risk of oxygen depletion.

In general, productivity rates do not provide clear regional or latitudinal patterns; specific production rates appear to be primarily influenced by individual system parameters. Studies within regions show that production rates generally increase in a downstream direction (e.g., Naiman 1983), but are suspected to decline in large, deep rivers (Dodge 1989). One might expect productivity to be lowest in the northernmost river systems and greatest in the southernmost systems, but the scant data fail to either confirm or refute this trend. While most stream ecosystems exhibit a strong link between primary and secondary productivity, riverine "production" and success of anadromous fish may be more closely linked with factors such as quality of spawning substrate and hydrologic conditions, not to mention the various limitations expressed within the marine portions of the life history of *S. salar*.

Diversity

For these systems, there are very few data related to biological diversity, an important and popular topic. Unfortunately, few, if any, comprehensive surveys have been done on regional diversity trends. O'Connell and Andrews (1996) remarked on the "paucity" of information on benthic macroinvertebrates in Newfoundland river systems and Petersen et al. (1995) noted that "no detailed benthic community studies" had been done on Icelandic and Nordic-alpine rivers. Stout and Vandermeer (1975) reported on the lack of any trend related to species richness of rheophilic insects in mid-latitudinal systems, but data revealing any trends (or lack thereof) across the entire range of *S. salar* remain inaccessible. Furthermore, anthropogenic disturbances have made it difficult to ascertain natural variations in biological diversity.

Riparian zones

Riparian zones serve as vital links between terrestrial and aquatic ecosystems. For the purposes of this paper, the riparian zone is defined as the terrestrial area within which soil and vegetation are influenced by river water on an annual basis (Naiman and Décamps 1990, 1997; Naiman et al. 1998*a*). These zones serve a variety of ecological functions and processes including bank stabilization, control of material movement, regulation of streamside microclimates, fil-

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Table 3. Selected major land uses and their impacts on lotic ecosystems.

Major land use	Impact	Location/example
Forestry and agriculture	Increased temperature; erosion; decrease in allochthonous inputs; increase in streamflow; dissolved nutrient concentration is correlated with cultivation and fertilizer application	European forests along Atlantic salmon rivers have been cleared extensively for agriculture since the Middle Ages
Industrialization and regulation	Temperature modification; eutrophication; overall reduction in discharge and sediment delivery	By 1860, 50% of salmon habitat in eastern North America (Region I) has been eliminated by damming and pollution associated with industrialization; another 25% has seen appreciable reductions in fish production capacity
Urban development	Frequency/magnitude of flooding is altered; increase in contaminant inputs; channel morphology is altered leading to simplification and loss of spawning and rearing habitat	>75% of the human population in the U.S.A., Canada and western Europe live in urban areas; urbanization is a major impact in Regions I and V

tration of nutrients, and the provision of allochthonous inputs (e.g., leaves, needles, and coarse wood). Along Atlantic salmon rivers, riparian vegetation reflects primarily the disturbance-oriented nature of the active channel and the floodplain and secondarily local forest vegetation. Species occurrence and relative abundance in many of the riparian zones depend primarily on life history characteristics of individual tree species (e.g., tolerance to inundation, capacity of damaged trees to regenerate, branch flexibility, root form, leaf form, season of productivity, duration of seed germinability) and the physical habitat conditions of the flood plain (soil condition, soil type, temperature, flood duration, season, current velocity, and flood force; Ellenberg 1982; Dister 1983; Krause 1985; Naiman and Décamps 1997). *Salix* (willow), *Alnus* (alder), *Betula* (birch), *Populus* (cottonwood, aspen, and other poplars), *Fraxinus* (ash), and *Fagus* (beech) represent typical riparian tree genera, many of which exhibit life history strategies (e.g., flexible stems, asexual reproduction) which allow them to persist in areas of varying disturbance. All regions maintain riparian tree cover with populations of many of the above species, except Region III (Iceland and Greenland), which is composed primarily of low growing woody shrubs and grasses.

A number of other generalities can be drawn regarding Atlantic salmon river riparian zones. The surrounding forests range from coniferous to broad-leaved deciduous forest. In general, the proportion of coniferous species increases as one moves north in latitude. This has implications for food webs given the differential in litter and woody debris decomposition rates and in detrital food quality between deciduous and coniferous stands. Organic matter from deciduous trees is generally more labile than coniferous-based detritus (Melillo et al. 1983; Webster et al. 1987). Accordingly, coniferous species, at least within the range of *S. salar*, are generally more decay resistant than deciduous members. As such, coniferous species may represent a more refractory source of organic matter but a more stable source of structurally important large woody debris (LWD).

Much of the natural riparian component of Atlantic salmon river systems has been altered considerably by human activities. Shifts in relative abundance of certain size-classes and species of riparian trees may have long-term implications for the structure and function of Atlantic salmon rivers. For instance, riparian systems which have been altered may be heavily represented by early-successional species which are typically a less important source of LWD.

Land use and impacts

Many Atlantic salmon rivers have received extensive anthropogenic modifications (Dynesius and Nilsson 1994). The catchments of western Europe and New England are heavily populated and have been affected by a range of stresses associated with agriculture, industrialization, and urbanization. Land use practices have resulted in increasingly rapid and long-lasting changes in channel morphology, hydrology, and water quality (Table 3). Although there are significant differences in climatic, physiographic, and ecological conditions among different regions, certain patterns of anthropogenic disturbance (e.g., forest clearing, urbanization, river regulation, etc.) are ubiquitous.

Forestry and agriculture. Forest clearing has been widespread throughout western Europe and eastern North America, to the extent that few Atlantic salmon rivers drain catchments with intact natural or late-successional forests. European forests have been cleared extensively for agriculture and timber since the Middle Ages and approximately 1×10^5 km^2 were cleared in northeastern North America by 1776 (Williams 1990). Between 1860 and 1978, an additional (estimated) 1.6×10^6 km^2 were converted to regular cropping in North America and 2.2×10^5 km^2 were converted in Europe (Richards 1990). Conversion of forest to cropland decreases vegetative cover and reduces infiltrative capacities, particularly where fields are tilled in fall and left bare throughout the winter and early spring months during peak flow season (Miller 1990). Associated increases in surface runoff entail increased stormflow peaks and decreased baseflow, as well as increases in temperature, siltation, and nutrient flux (Bormann et al. 1969; Likens et al. 1970; Likens 1984). Export of dissolved nutrients is correlated with area under cultivation and rates of fertilizer application (Hill 1978; Miller et al. 1982; Neilsen et al. 1982). Pesticides typically occur in agricultural streams during spray season, but some compounds are persistent enough in soils to leach continually throughout the year (Frank et al. 1982).

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Surface runoff represents the most important pathway for agricultural pollutant inputs (Frank et al. 1982; Miller et al. 1982) and effects are therefore likely to be greatest in areas where clay soils or thin soils overlay rocky terrain.

Industrialization and hydroelectric power. With factories, mills, and foundries typically built near flowing water, salmon rivers of Europe and North America have been further impacted by industrialization. Industrial production and power generation have resulted in point and nonpoint source pollution and extensive damming and diversion of rivers. Rivers of western Europe and Scandinavia have been dammed for centuries (Ladle and Westlake 1995; Petersen et al. 1995), to the extent that, as early as the 17th and 18th centuries, legislation such as the French Bearnais statute (1662) and the edicts of Spain's Carlos IV (1790s) were deemed necessary to protect migratory passage for salmon (Netboy 1968). The scale of European river modification increased significantly with the Industrial Revolution (Allan 1995) and dam-building technologies were then transported to North America. By 1850, an estimated 50% of salmon habitat in eastern North America was eliminated by damming and pollution associated with agriculture and industry, with an additional 25% being appreciably reduced in production capacity for salmon (Legget 1975). Today there are more regulated rivers than naturally flowing ones in the United States (Benke 1990; Hydrodata 1995; Naiman et al. 1998*b*. Similarly, the majority of watercourses in western Europe (Region V) and Scandinavia (Region IV) are regulated (Petts 1984; Petersen et al. 1995).

The effects of major impoundments include overall reductions in discharge and sediment delivery downstream, as well as dampening of temperature and flow variability (Ward and Stanford 1979; Richards 1992; Allan 1995). Specific impacts will vary according to the location, size, and nature of the reservoir (e.g., hypolimnetic vs. epilimnetic), as well the natural hydrologic regime and sedimentology of the river. Effects may be felt many kilometres downstream from dams (Webster et al. 1995).

Urban development. Urbanization has resulted in massive changes in the physical landscapes and hydrologic regimes of western Europe and North America. The removal of natural vegetative cover in favor of impervious surfaces, the installation of storm sewer systems, and the channelization of streams entail a more severe manifestation of the hydrologic symptoms of forest clearing. Accordingly, frequency and magnitude of flooding in urban streams increase with percent catchment imperviousness (Leopold 1968; Klein 1979). Hydrologic effects are compounded by contaminant inputs from urban runoff and sewer outfalls, which contain a complex mixture of conventional, metal, and organic contaminants (Marsalek 1986, 1990). In the United States, Canada, and most of the western European nations, greater than 75% of the population lives in urban areas (Berry 1990). As trends toward increased urbanization and suburban sprawl continue, salmon rivers will be increasingly impacted.

Within the natural range of Atlantic salmon, only the most northern rivers have been relatively unaffected by forestry, agricultural, industrial, and urban development. However, these rivers may be particularly susceptible to effects of climate change (Minns et al. 1992) and long range transport of atmospheric pollutants (Wania and Mackay 1993).

Case studies

The following case studies are provided as illustrations of typical systems within the natural range of *S. salar*. These rivers are certainly not representative of all rivers within each region and may not be the most important. They were, however, selected to show real examples of salmon-bearing systems within three of the regions reviewed in this article.

The River North Esk, England

While there is considerable variation among the rivers of western Europe (Region IV), it is useful to select examples which provide contrast to rivers of other regions. The River North Esk is a small river system which arises in Invermark Forest in northeast Scotland and flows eastward about 50 km to enter the North Sea between Aberdeen and Dundee. Despite its small size, it is one of Scotland's major salmon rivers and, indeed, has been a site for extensive research into natural history and stock dynamics (Shearer 1992).

The River North Esk and its 75 total tributaries drain 732 km^2 with an elevation drop of 750 m. Average flow is 13 $m^3 \cdot s^{-1}$ with a range of 2–280 $m^3 \cdot s^{-1}$; peak flows occur in December with low flows in July (Ward 1981). Lining the riverbanks of the upper reaches are scattered patches of birch (*Betula pendula*) and alder (*Alnus glutinosa*) which give way to beech (*Fagus sylvatica*) in the middle reaches. The lower third of the river is largely agricultural.

During the years 1985 and 1986, water temperature in the river ranged from 2 to 16°C ($\bar{x}$ = 7.7°C) while pH ranged from 6.9 to 8.8 ($\bar{x}$= 7.65). Two year ranges and means (reported in parentheses) for other water quality parameters were 87.2–123.0% (99.7) for dissolved oxygen (DO), 0.0–4.8 mg $O_2 \cdot L^{-1}$ (2.2) for biological oxygen demand (BOD) and 0–11 mg $O_2 \cdot L^{-1}$ (4.0) for suspended solids. Ranges for nitrogen concentrations were 0–0.11 mg $N \cdot L^{-1}$ (0.03) for ammonia and 0.75–3.78 mg $N \cdot L^{-1}$ (1.97) for total oxidized forms (i.e., NO_3 and NO_2; Shearer 1992).

Agriculture and water withdrawal are the primary human impacts on the catchment. Silage effluent and pesticide discharge from extensive agriculture in the lower reaches occasionally causes fish kills and soil erosion resulting from land uses occasionally deposit layers of silt over gravel. Water is abstracted in the upper reaches at Loch Lee, which has been converted to a reservoir, as well as pumped from along the length of the river for irrigation. Industry on the river is slight (two distilleries) and there has been little forestry development.

Rivers in Scotland typically have yielded more Atlantic salmon than elsewhere in Great Britain (Netboy 1980). The River North Esk itself is the most productive on the east coast (catch per kilometre), a fact attributed to the high availability of spawning gravel in the mainstream and tributaries (Shearer 1992). High water quality and lack of substantial human impact relative to other rivers in Region V may also be important. As long as agriculture remains the primary human impact, water quality monitoring and bank erosion control may be the most effective management strategies in the catchment.

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Rickleån River, Sweden

Located roughly 80 km north of the town of Umeå, Sweden, the Rickleån River flows into the Gulf of Bothnia. This medium-sized river has an average discharge of 16 $m^3 \cdot s^{-1}$ (range of 3–180 $m^3 \cdot s^{-1}$) and flows within a boreal forest zone (as defined by Sjörs 1963) dominated by spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The primary floodplain tree species are typical of other Atlantic salmon rivers, including alder (*Alnus incana*), birch (*Betula pubescens*), and willow (*Salix* spp.).

With a PO_4–P range of 1–12 $\mu g \cdot L$ and a NO_3–N range of 0–0.03 $\mu g \cdot L$, the Rickleån is best described as oligotrophic (Karlström 1976; R.C. Petersen, Jr., unpublished data). Rickleån pH ranges between 6.0 and 7.0 (Göthberg and Karlström 1975). Water in the Rickleån is clear and flows over a granite/gneiss crystalline rock substrate. This river maintains a 0.3% gradient, considered quite steep (Södergren 1974). Several rivers within the vicinity of the Rickleån are also quite steep and many, including the Rickleån, have been regulated, both factors contributing to the region's "Staircase of Power" nickname.

As a result of the steep gradient, the river has little floodplain and minimal sinuousity (Ulfstrand 1968). Turbulent, abrasive currents seem to be cause for high organic matter decomposition rates (0.83–0.95% d^{-1}). R.C. Petersen, Jr. (unpublished data) measured gross primary production in the Rickleån as approximately 98 mg $C \cdot m^{-2} \cdot d^{-1}$ in August and approximately 87 mg $C \cdot^{-2} \cdot d^{-1}$ in September, generally considered low.

Anthropogenic disturbance plays an important role in Rickleån ecology. The river itself consists of three tributaries emptying into a lake, the Bygdeträsket, regulated by a dam. From there, the Rickleån proper flows to the sea, with five power stations along its course. In addition to being regulated, this system suffers from heavy metal pollution in its lower reaches (Södergren 1974). Nonanadromous brown trout (*Salmo trutta*) and anadromous *S. salar* dominate the fish community.

The Rickleån provides an example of the factors which often dictate success in anadromous salmonids. The system does not exhibit high primary productivity but does consistently provide desirable spawning substrates, moderate flows, and clear, oxygen-rich water. While regulation has compromised unabated access, the river continues to summon the annual return of *S. salar*.

Moisie River, Québec

The biophysical characteristics of the Moisie River, Québec, have been well documented (Naiman 1982, 1983; Naiman et al. 1987; Naiman and Link 1997). The Moisie River empties into the north shore of the Gulf of St. Lawrence, draining a catchment of 19 871 km^2. This subarctic, precambrian Shield region is forested with typical boreal species: black and white spruce (*Picea mariana, P. glauca*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), speckled alder (*Alnus rugosa*), and willow (*Salix* spp.). The area receives approximately 1.2 m of precipitation annually, which is evenly distributed throughout the year and occurs primarily as snow from October through April. Mean annual air temperature is 1°C and growing season (mean daily temperature > 5.6°C) is 105 d. The Moisie is a relatively pristine river, as less than 1% of catchment area has been subjected to anthropogenic disturbance.

Mean annual discharge on the main stem of the Moisie (stream order 9) is 466.1 $m^3 \cdot s^{-1}$ and the gradient is 0.16%. High flows representing 50% of annual discharge occur during April and May freshets, whereas January and February flow volumes represent only 3–5% of annual maxima. Water temperatures range from 0.1 to 21.8°C and substrate is primarily sand and cobble. Alkalinity ranges from 0.0 to 17.0 $mg \cdot L^{-1}$ as $CaCO_3$ and pH values range from 6.3 to 7.1. Streams in this area have relatively low concentrations of NO_3–N (20–43 $g \cdot L^{-1}$) and phosphorus (11–29 $g \cdot L^{-1}$) and relatively high concentrations of DOC (10–15 mg $C \cdot L^{-1}$).

Naiman et al. (1987) reported significant trends with stream order for organic carbon dynamics, as related to changes in physical gradients, channel dimensions, hydrology, and riparian influences. As stream order increased, total C inputs (i.e., precipitation, throughfall, primary production, and allochthonous matertials) decreased, followed by a gradual increase due to greater primary production in streams >6th order.

Standing stock of C decreased exponentially downstream and total C outputs (i.e., respiration, leaching, methane evasion, and insect emergence) increased slightly. Most organic C was stored in 1st–3rd order streams, whereas the majority of C was metabolized in 7–9th order rivers. Percentage transmission of PAR to benthic substrates are significantly correlated with stream order, due to the fact that shading decreases, yet mean depth remains constant (<2 m) (Naiman and Link 1997). The majority of organic matter inputs result from autotrophic production, although fluvial transport of organic C to the Gulf of St. Lawrence was nearly three times that of total annual inputs, demonstrating that groundwater inputs of DOC are exceedingly important (Naiman et al. 1987).

Concluding remarks

The preceding case studies describe typical Atlantic salmon rivers in three of the five regions discussed in this paper. With the possible exception of the Moisie, these studies analyze rivers which have experienced marked declines in natural salmon production. Still, even the Rickleån, with a reportedly meager run of salmon and a series of dams, continues to provide some of the necessary ecological parameters which beckon the return of the fish. This paper has addressed some of the biophysical factors which provide the template upon which *S. salar* relies.

We have addressed patterns in biophysical influences on river systems within each of five regions. Among the various influences, biotic processes, such as primary production, may explain some regional variation in salmon abundance and success. However, success in anadromy and riverine "production" of anadromous salmonids is also reliant on factors such as discharge, substrate, and temperature regimes. A fundamental understanding of the natural variation of riverine conditions is necessary for the development of a restoration strategy guided toward life history and evolutionary strategies of *S. salar*; the most effective strategies will be those that consider the unique behavioral and physiological adaptations of local salmon populations.

Salmo salar has evolved to river conditions over a period best measured in tens of thousands of years. Over a relatively short time, anthropogenic disturbances have altered

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many of the biological and physical conditions upon which Atlantic salmon adaptations have been based. Monitoring riverine conditions against a background of a highly variable biophysical environment remains a major challenge for managers and researchers alike — one that must be resolved on a broad spatial scale if the long-term integrity of Atlantic salmon rivers is to be maintained.

The ecological consequences of regional differences in catchment characteristics, as well as latitudinal gradients in discharge patterns and temperature, have important implications for the management, restoration, and conservation of Atlantic salmon rivers. The North Atlantic Ocean (and its adjacent seas) is a heterogeneous region with substantial biophysical variability both within and among catchments. Management philosophies and restoration and conservation strategies embracing this natural variation will be the most successful in the long term.

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Why aren't there more Atlantic salmon (*Salmo salar*)?

Donna L. Parrish, Robert J. Behnke, Stephen R. Gephard, Stephen D. McCormick, and Gordon H. Reeves

Abstract: Numbers of wild anadromous Atlantic salmon (*Salmo salar*) have declined demonstrably throughout their native range. The current status of runs on rivers historically supporting salmon indicate widespread declines and extirpations in Europe and North America primarily in southern portions of the range. Many of these declines or extirpations can be attributed to the construction of mainstem dams, pollution (including acid rain), and total dewatering of streams. Purported effects on declines during the 1960s through the 1990s include overfishing, and more recently, changing ocean conditions, and intensive aquaculture. Most factors affecting salmon numbers do not act singly, but rather in concert, which masks the relative contribution of each factor. Salmon researchers and managers should not look for a single culprit in declining numbers of salmon, but rather, seek solutions through rigorous data gathering and testing of multiple effects integrated across space and time.

Résumé : Les effectifs de saumon de l'Atlantique (*Salmo salar*) sauvage anadrome ont diminué notablement dans toute l'aire de répartition naturelle de l'espèce. On a observé des baisses étendues et même la disparition des remontes dans les rivières à saumon en Europe et en Amérique du Nord, surtout dans les parties méridionales de l'aire de répartition de l'espèce. Bon nombre de ces déclins ou de ces disparitions sont attribuables à la construction de barrages sur les cours principaux des rivières, à la pollution (notamment aux pluies acides) et à l'assèchement complet de certains cours d'eau. On pense aussi que les déclins qui se sont produits depuis les années 1960 jusque dans les années 1980 pourraient aussi être dus à la surpêche et, plus récemment, à l'altération des conditions océaniques et à l'aquaculture intensive. La plupart des facteurs influant sur les effectifs du saumon n'agissent pas seuls mais de concert avec d'autres facteurs, ce qui masque la contribution relative de chacun de ces facteurs. Les chercheurs et les gestionnaires qui s'intéressent au saumon ne devraient pas chercher une cause unique qui serait responsable du déclin des effectifs de saumon, mais plutôt rechercher des solutions en recueillant des données de façon rigoureuse et en examinant des effets multiples considérés dans le temps et dans l'espace.

[Traduit par la Rédaction]

Introduction

We want to know why aren't there more Atlantic salmon (*Salmo salar*)? The irony of this question is that Atlantic salmon are now more abundant than at any time previously. Virtually all (~98% of the biomass) of the present abundance is because of the artificial culture of salmon as a food fish, whereas wild Atlantic salmon numbers have been in a general decline. In this paper, we examine the geographic distribution of extirpations and declines in anadromous populations of Atlantic salmon (omitting aquaculture and nonanadromous populations) and establish the reasons for these changes.

We cannot determine exactly how many salmon existed 400 years ago, or even presently, because our estimates of abundance are based mostly on catch data for which fishing effort is often inaccurate (Shearer 1992). The total North Atlantic commercial salmon catch from 1960 through 1987 indicates a high abundance cycle from the mid-1960s to the mid-1970s, with catch maxima of about 12 000 t in 1967 and 1973 (Mills 1989). Numbers of salmon returning to home rivers declined precipitously during this time frame

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D.L. Parrish.[1] Vermont Cooperative Fish and Wildlife Research Unit,[2] School of Natural Resources, University of Vermont, Burlington, VT 05405, U.S.A.
R.J. Behnke. Colorado State University, Department of Fishery and Wildlife Biology, Fort Collins, CO 80523, U.S.A.
S.R. Gephard. Connecticut Department of Environmental Protection, Fisheries Division, P.O. Box 719, Old Lyme, CT 06371, U.S.A.
S.D. McCormick. Conte Anadromous Fish Research Center, USGS/Biological Resources Division, P.O. Box 796, Turners Falls, MA 01376, U.S.A.
Gordon H. Reeves. USDA Forest Service, 3200 Jefferson Way, Corvallis, OR 97331, U.S.A.

[1]Author to whom correspondence should be addressed. e-mail: dparrish@nature.snr.uvm.edu
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and now most fisheries are closed. Although current abundance estimates must come from variable data sources (e.g., adult escapement, smolt production), there is no question that in general salmon numbers are further declining during the time of fishery closures, indicating more than overfishing is responsible for continued declines.

Current status of Atlantic salmon

We reviewed available information to develop maps showing the current status of wild anadromous Atlantic salmon in the world. Status categories for these maps are based solely on current numbers of adults returning to rivers. Categories were: Extirpated (E) — no returns for at least 10 years, Extirpated with restoration (E/R) — no returns for many years followed by the initiation of a program to reintroduce salmon, Declining (D) — long-term decrease (>10 years) in numbers of adults returning, or Stable (S) — no consistent decline in numbers of adults returning during the last 10 years. We determined categories with substantial input of participants from Europe and North America at the March 1997 workshop as well as other biologists polled after the meeting. This approach does not allow for determining the status of salmon in every river historically supporting salmon; nonetheless, employing our approach allows us to portray patterns of salmon status across broad geographical areas, which was our ultimate goal.

Distributions of salmon populations in Europe (Fig. 1 and Table 1) and North America (Fig. 2 and Table 2) indicate many rivers historically supporting Atlantic salmon populations on these continents have experienced extirpation or great declines. (Note: Fig. 1 does not show the entire range of Atlantic salmon, which extends to the Pechora River, Russia, northeast of the White Sea. Rivers not shown on the European map are considered stable.)

Globally, most watersheds in the southern portions of the salmon range are extirpated (Figs. 1 and 2). It is not coincidental that these areas have the highest human population densities and have experienced the greatest environmental damage resulting from human activity. In Europe, three distinct tiers emerge; in the north, populations are stable; at intermediate latitudes, populations are declining; and in the south, populations are largely extirpated. Restoration efforts in Europe are few and scattered across the tiers.

North American populations follow a pattern similar to that of Europe in that northern populations (Canadian) are stable and southern populations are extirpated (Fig. 2). A major difference between distributions in North America and Europe is that proportionally more restoration efforts are in place in North America (e.g., most U.S. populations were extirpated and most large watersheds are targeted for restoration). A few small U.S. drainages near the Canadian border retain native, albeit, declining runs. Generally, Canadian rivers range from stable populations in the north, to declining populations in the midsection, to extirpated runs (including those under restoration) in the southern reaches. A deviation from the European pattern in North America is the area along the St. Lawrence in middle latitudes, where rivers are extirpated with restoration. The St. John in New Brunswick and many southeast Nova Scotia rivers are examples of rivers that are declining, which follows the pattern shown at middle latitudes of the salmon distribution in Europe.

What causes declines in Atlantic salmon abundance?

It is unmistakably evident from the European and North American maps that the current status of many salmon rivers is declining or extirpated. What factors are responsible for the declines and extirpations of Atlantic salmon globally? Armstrong et al. (1998: fig. 1) provide a useful depiction of hierarchical effects on Atlantic salmon populations, based on spatial and temporal scales. Clearly, many causal factors act in concert often masking the contribution of individual components and thereby complicating our ability to discern individual mechanisms (Armstrong et al. 1998). In cases of extirpation, it is possible to identify some of the single factors, but in currently declining populations multiple factors are more likely responsible. Below we provide descriptions of some of the causes implicated as contributing to the demise of Atlantic salmon populations as related to the status of salmon in Europe and North America (Figs. 1 and 2). Factors such as competition (Fausch 1998), introductions (Youngson and Verspoor 1998), pathogens and diseases (Bakke and Harris 1998), predation (Hansen and Quinn 1998; Mather 1998), prey (Poff and Huryn 1998; Hansen and Quinn 1998), and ocean conditions, especially related to thermal distributional patterns (Friedland 1998) are likely to contribute to declines, but not necessarily extirpations of Atlantic salmon populations. There are questionable effects of global warming and intensive aquaculture that could alter the long-term sustainability of salmon populations (Wilzbach et al. 1998), but the effects are too subtle or undetermined to attribute to the patterns of extirpation and declines of Atlantic salmon populations.

The construction of dams without fish passage has extirpated entire salmon runs in many rivers and is listed as the single major cause of salmon extirpations (MacCrimmon and Gots 1979). In the U.S., dams caused the local extinction of Atlantic salmon on the Connecticut and Merrimack rivers and had negative consequences in several Maine rivers (Moffitt et al. 1982). Extirpations because of dams have occurred throughout Canada (Dunfield 1985), Spain (Garcia de Leaniz and Martinez 1986), Czechoslovakia, Denmark, Finland, France, Germany, and Sweden (MacCrimmon and Gots 1979). Lower mainstem dams on major rivers occur in areas that correspond to red (extirpated) or red-striped (extirpated with restoration) sections on the maps of Europe and North America (Figs. 1 and 2). The density of dams generally corresponds to human population density.

Sewage, which included human waste, was one of the major pollutants that reduced numbers of salmon in the River Thames in England (MacCrimmon and Gots 1979). Industrial pollution in the rios Miera and Besaya in Spain (Garcia de Leaniz and Martinez 1986) and pesticides in several New Brunswick (Canada) rivers (Elson 1967) were to blame for elimination of salmon. High levels of pollution occurred in all of the European countries listed above where dams were constructed.

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Fig. 1. Map of Atlantic salmon population status for major watersheds throughout original range in Europe. Numbering of watersheds is in Table 1. Note: Distance to Iceland is not to scale and range in Russia is truncated.

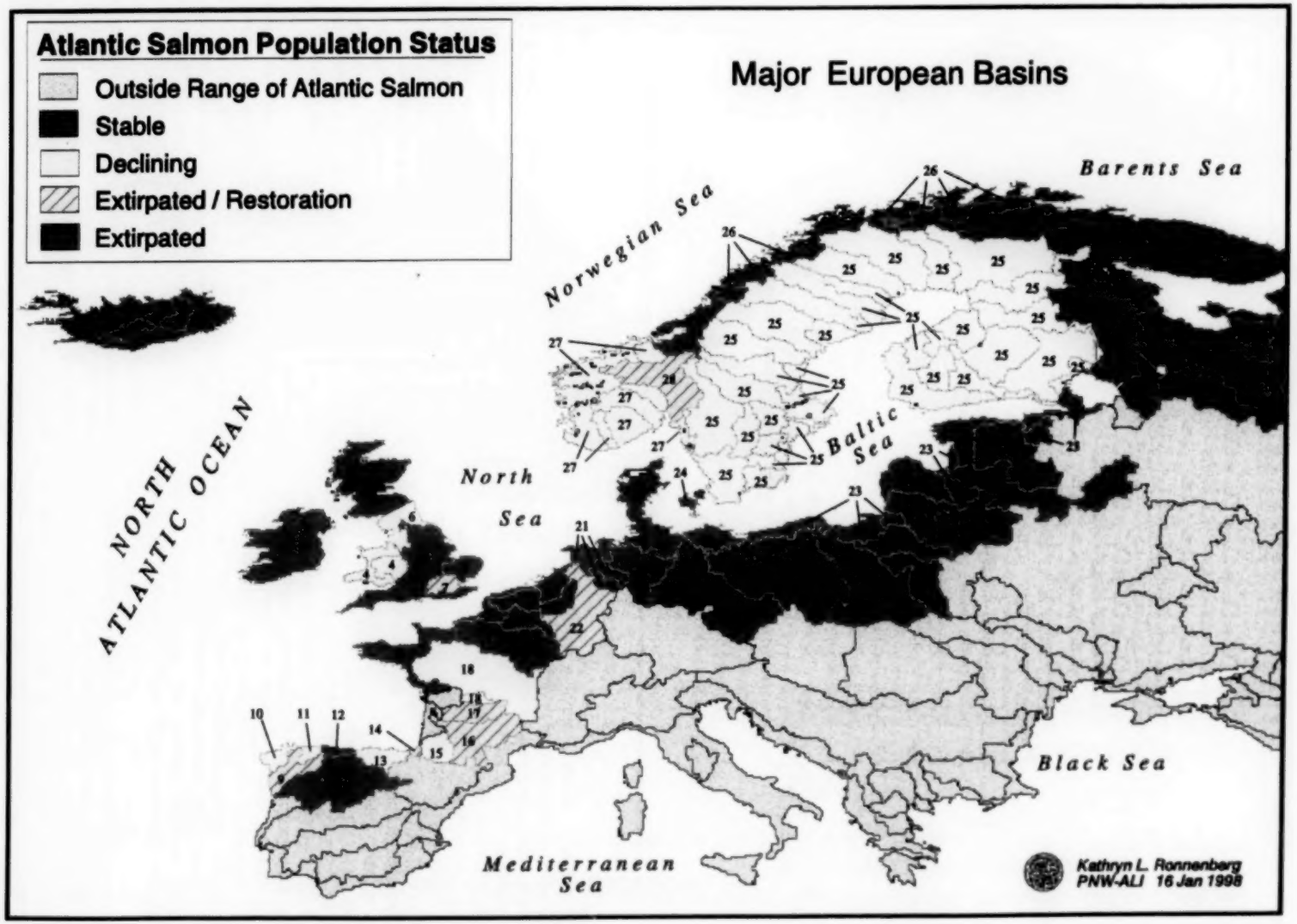

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Table 1. Current status of Atlantic salmon populations in the major river basins of Europe and Iceland.

Number	River basin or region (country)	Status
1	Iceland	S
2	Ireland (Shannon, Erne, and Lee rivers: D)	S
3	Scotland	S
4	Wales	D
5	Southern and Central England	E
6	Northern England	D
7	Thames River (England)	E/R
8	Duoro River (Portugal and Spain)	E
9	Mino River (Portugal and Spain)	E/R
10	Galicia (Spain)	D
11	Austurias (Spain)	D
12	Cantabria (Spain)	D
13	Cantabria/Vasco (Spain)	E
14	Rio Bidasoa (Spain)	E/R
15	Adour River (France)	D
16	Garronne River (France)	E/R
17	Dodogne River (France)	E/R
18	Loire River (France)	D
19	Britanny and Normandy (France) (Orne, Vire, and Rance rivers: E)	S
20	Seine River (France)	E
21	Coastal N. France, Belgium, Netherlands, and Germany	E
22	Rhine River (Germany and Switzerland (not shown))	E/R
23	Southern Baltic (Germany, Poland, Lithuania, Latvia, Estonia, Russia)	E
24	Denmark	E
25	Northern Baltic (Sweden and Finland)	D
26	Northern Norway, Finnmark, Russia	S
27	Southern Norway	D
28	Glama River (Norway)	E/R

Acid pollution affects salmon in northern Europe and North America and presents a more complex spatial pattern. In Norway, salmon populations in 25 rivers were driven to extinction because of lethal pH levels (Hesthagen and Hansen 1991) and salmon rivers have been negatively affected in Nova Scotia, Canada (Lacroix and Townsend 1987). Acid rain is substantially different from dams or pollution in that acid rain is the result of industrial emissions often far from the point of deposition. In Europe, countries on the southern side of the Baltic Sea are responsible for creating acid rain in Sweden and Norway and in North America, industrial activity in midwestern U.S. and Canada creates most of the problems for Canadian rivers. Consequently, the large-scale effects of acid rain are more difficult to prove than the river-level effects of dams or direct-input pollution because of dispersion, prevailing weather patterns, and watershed geology. Therefore, acid rain, because of inconstant factors, may be a major component responsible for the more variable patterns of salmon status at the mid-latitudes than those in the north and south (Figs. 1 and 2).

With the exception of dams and water pollution, examples of habitat degradation or improvements that have affected adult Atlantic salmon populations are, to our knowledge, nonexistent. Potentially one of the most severe alterations of fish habitat is flow depletion from withdrawals for industrial, domestic, and agricultural use. When a river is completely dewatered the obvious result is no fish. The Nepaug River, Connecticut, U.S.A., a former salmon river, has no flow at its mouth because all water is diverted to supply drinking water to the City of Hartford (Stephen R. Gephard, personal observation). However, most water withdrawals divert only a portion of the total stream flow and assessing the impacts on salmon in relation to magnitude and timing of the altered hydrograph is not a simple matter. The nature of the problem has been well described and potential impacts have been speculated upon for streams in Scotland (Mills 1980), England (Dill et al. 1975; Harris 1980), Ireland (Piggins 1980), and the Rio Ascon in Spain (Garcia de Leaniz, Servicio de Montes, personal communication), all areas of significant urbanization.

The effects of commercial fishing are also variable and often unpredictable. Reasons for this include: (*i*) home-water vs. distant-water (intercepter) fisheries, (*ii*) interplay of changing ocean currents and catch, (*iii*) inaccurate catch and effort data, and (*iv*) compensatory mortality mechanisms of salmon. However, some examples showing the effects of fisheries follow: numbers of grilse returning to 20 Newfoundland rivers have generally increased following the closures of Newfoundland fisheries in 1992 and 1993 (O'Connell 1997) and adult returns increased in the Highland's River where returning fish were monitored the years after the 1992 fishing moratorium (Gibson et al. 1996). Regardless, given that the moratorium in major fisheries (Can-

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Fig. 2. Map of Atlantic salmon population status for major watersheds throughout original range in North America and Greenland. Numbering of watersheds is in Table 2. Note: Distance from Greenland to North America not to scale.

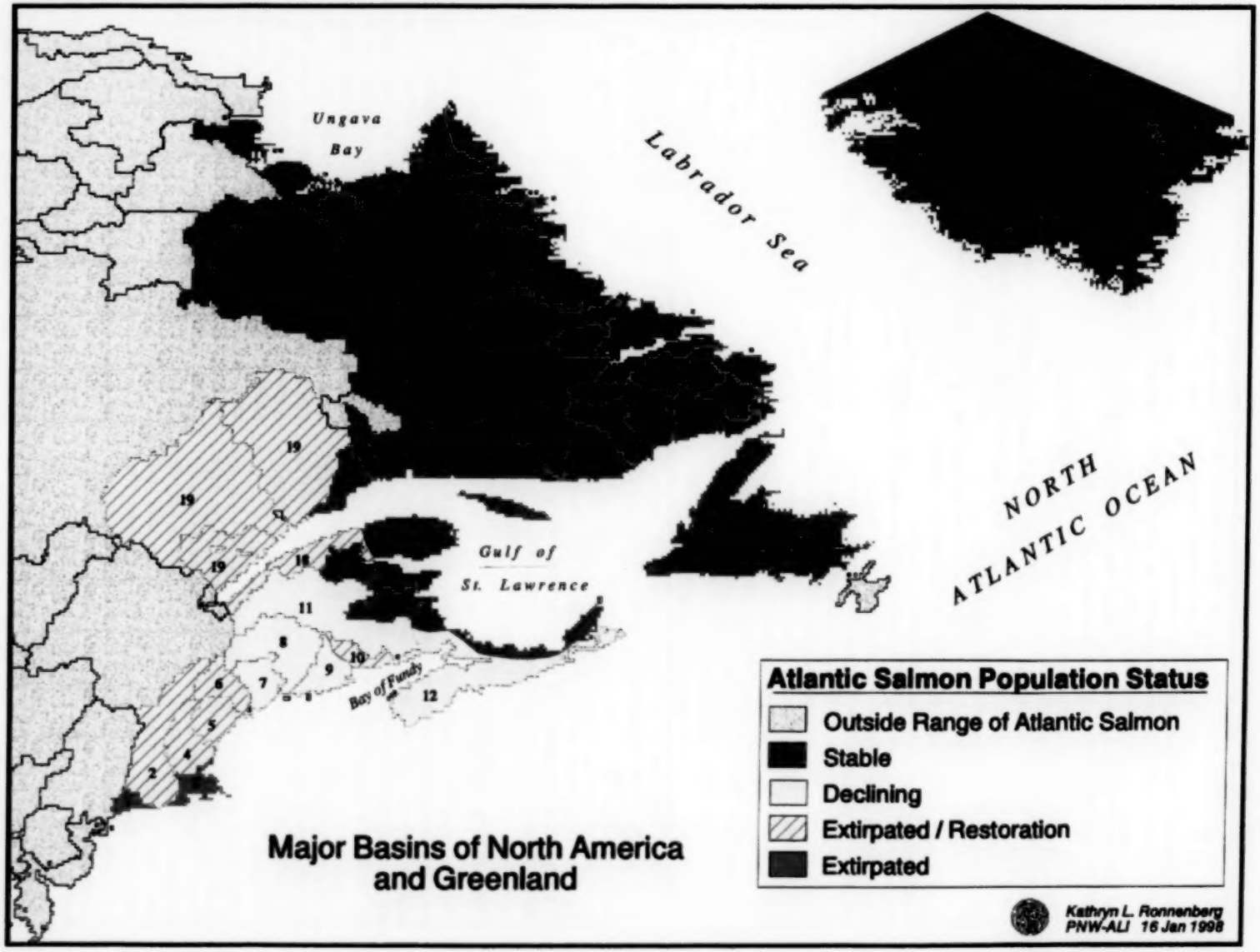

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Table 2. Current status of Atlantic salmon populations in the major river basins of North America (U.S.A. and Canada) and Greenland.

Number	River basin or region (state or province, country)	Status
1	Housatonic River and coastal drainages (CT, U.S.A.)	E
2	Connecticut River (U.S.A.)	E/R
3	Coastal drainages (CT, RI, and MA, U.S.A.) (Pawcatuck River, RI: E/R)	E
4	Merrimack River (MA and NH, U.S.A.)	E/R
5	Saco River and coastal drainages (NH and ME, U.S.A.)	E/R
6	Androscoggin River (ME, U.S.A.)	E/R
7	Kennebec, Sheepscot, Ducktrap rivers (ME, U.S.A.)	D
8	Penobscot River (ME, U.S.A.)	D
9	Downeast Rivers (Dennys, Machias, Narraguagus, Pleasant, E. Machias) (ME, U.S.A.)	D
10	St. Croix River (ME, U.S.A., and NB, Canada) (Western NB coastal drainage: D)	E/R
11	St. John River (NB, Canada)	D
12	Bay of Fundy (NB, Canada) and Southeast and Atlantic Nova Scotia (Canada)	D
13	Gulf of St. Lawrence (NB and NS, Canada)	S
14	Miramichi River (NB, Canada)	S
15	Nepisiguit River and coastal drainage (NB, Canada)	S
16	Restigouche River (NB, Canada)	S
17	Gaspé Peninsula drainage (PQ, Canada)	S
18	South Shore St. Lawrence (PQ, Canada)	E/R
19	N. Shore St. Lawrence River (PQ, Canada)	E/R
20	N. Shore St. Lawrence (PQ, Canada)	S
21	Anticosti Island (PQ, Canada)	S
22	Labrador (NF, Canada)	S
23	Ungava River drainage (PQ, Canada)	S
24	Greenland	S
25	Newfoundland (Canada)	S

Note: States in the U.S.A. are as follows: CT = Connecticut, MA = Massachusetts, ME = Maine, NH = New Hampshire, RI = Rhode Island. Provinces in Canada are as follows: NB = New Brunswick, NF = Newfoundland, NS = Nova Scotia, PQ = Quebec.

ada, West Greenland, and the Faroes Islands) is less than 10 years old, we cannot address the effects of fisheries on salmon abundances on a global scale (Figs. 1 and 2).

Concluding remarks

Efforts in the past have attempted to summarize the status of Atlantic salmon populations regionally (e.g., Atkins 1874; Kendall 1935; Garcia de Leaniz and Martinez 1986) and globally (Netboy 1968; MacCrimmon and Gots 1979). In this paper, we specifically provided information regarding the declines and extirpation of salmon on a global scale, but a more comprehensive treatment is warranted. The information presented shows that Atlantic salmon stocks continue to decline despite the efforts of many nations to study, protect, and restore runs.

Our charge was to address the spatial pattern and reasons for declines in populations of wild Atlantic salmon. We were able to do that in some cases where single factors could be identified (i.e., dams, pollution, and dewatering) for specific sites. The available evidence allows us to speculate that more dams result in fewer salmon and that greater densities of humans near salmon rivers also result in fewer salmon. However, we can not link cause and effect for most declines because they are the result of multiple factors and we do not have the data that discriminate factors on scales of space or time. Consequently, we can not allocate the proportional impacts of multiple factors contributing to the demise of salmon populations and without this information we can only guess at specific causes.

To determine the specific contributions of multiple factors, we need to establish sampling programs that provide definitive results. If data were collected rigorously and comparably throughout the Atlantic salmon range, we could, for example, perform meta-analyses, conduct experimental procedures to address specific questions, and expand the use of models to predict changes in salmon sustainability (Wilzbach et al. 1998). The onus is on researchers and managers to use newer rigorous methodologies, including developing effective sampling designs and incorporating adaptive management (Wilzbach et al. 1998), to determine why salmon have declined and continue to do so. By applying science to management at appropriate temporal and spatial scales (Armstrong et al.1998), and through concerted conservation efforts (Dodson et al. 1998; Wilzbach et al. 1998), we hope the status of many Atlantic salmon rivers reported here as declining or extirpated with restoration will be changed in years ahead to a new category of increasing abundances.

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Proactive responses to human impacts that balance development and Atlantic salmon (*Salmo salar*) conservation: an integrative model

Margaret A. Wilzbach, Martha E. Mather, Carol L. Folt, Andrew Moore, Robert J. Naiman, Alan F. Youngson, and James McMenemy

Abstract: Incorporating human impacts into conservation plans is critical to protect natural resources. Using a model that examines how anthropogenic changes might be proactively influenced to promote conservation, we argue that a denser human population does not spell inevitable doom for Atlantic salmon (*Salmo salar*). Humans affect the Atlantic salmon ecosystem deleteriously through landscape alteration, exploitation, external inputs, and resource competition. An intact ecosystem provides positive feedback to society by providing food, ecosystem services, and improving the quality of life. As Atlantic salmon and associated ecosystem benefits are increasingly valued by society, policies, laws, and regulations that protect salmon populations and habitats are codified into a "control system" or institutional infrastructure. Via research that helps maintain wild salmon populations and in informing the public about the benefits of a healthy Atlantic salmon ecosystem, scientists can influence public attitudes and facilitate the implementation of environmental policies that moderate harmful anthropogenic changes. Because exchange among scientists is of paramount importance in increasing our understanding of important interrelationships between humans and fish, we recommend the establishment of an international salmon organization for research.

Résumé : L'intégration des impacts anthropiques dans les plans de conservation est un facteur critique pour la protection des ressources naturelles. À l'aide d'un modèle qui examine la façon dont on pourrait influer sur les changements anthropiques pour promouvoir la conservation, nous soutenons que la densification de la population humaine n'est pas nécessairement catastrophique pour l'avenir du saumon de l'atlantique (*Salmo salar*). Les êtres humains ont un effet néfaste sur l'écosystème du saumon à cause de l'altération des paysages, de l'exploitation, des apports externes et de la concurrence pour la ressource. Un écosystème intact apporte à la société une rétroaction positive en fournissant de la nourriture et des « services écosystémiques », et en améliorant la qualité de vie. Le saumon de l'atlantique et ses retombées écosystémiques étant de plus en plus appréciés par la société, on codifie les lois, règlements et politiques en un « système de contrôle » ou une infrastructure institutionnelle. Grâce à la recherche qui aide à maintenir les populations sauvages de saumon, et en informant le public sur les effets positifs de la santé de l'écosystème du saumon, les scientifiques peuvent influer sur les attitudes des citoyens et faciliter la mise en oeuvre de politiques environnementales qui modèrent les effets anthropiques néfastes. Les échanges entre chercheurs étant d'une importance primordiale pour mieux comprendre les importantes relations entre les humains et les poissons, nous recommandons la création d'une organisation internationale de recherche sur le saumon.

[Traduction par la Rédaction]

Introduction

Identifying human impacts and demographic trends that affect key fish species such as Atlantic salmon, *Salmo salar*, and incorporating that information into a conservation and management strategy is critical to sustain and protect this valued natural resource. Unfortunately, exact prediction of stressors and subsequent ecosystem responses is not possible because of system complexity, natural variability, random variation, estimation errors, and incomplete information (May 1986). But even if predicting accurately in a complex world is futile, we can still identify important factors and project general trends that, via monitoring, can be evaluated and modified. Strengthening our abilities to proactively deal

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M.A. Wilzbach. Florida Center for Environmental Studies; Tarpon Bay Laboratory, 900A Tarpon Bay Road, Sanibel, FL 33957, U.S.A. e-mail: pwilzbach@olsusa.com
M.E. Mather. Massachusetts Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey – Biological Resources Division, Amherst, MA 01003, U.S.A. e-mail: mather@forwild.umass.edu
C.L. Folt. Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, U.S.A.
A. Moore. The Center for Environment, Fisheries, and Aquaculture, Lowestoft, NR330HT, U.K.
R.J. Naiman. School of Fisheries, University of Washington, Seattle, WA 98195, U.S.A.
A.F. Youngson. Scottish Office Agriculture, Environment, and Fisheries, Pitlochry, U.K.
J. McMenemy. Vermont Department of Fish and Wildlife, North Springfield, VT 05150, U.S.A.

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with future trends is vital for ecological understanding and successful natural resource stewardship. Furthermore, this information is critical for conservation-oriented development

One prediction that can be made with reasonable certainty, however, is that human impacts on the freshwater, estuarine, and marine components of Atlantic salmon ecosystems will continue to intensify as the human population grows. The relative contribution of anthropogenic changes, natural climatic events, and other abiotic and biotic factors in the large decline in abundance of wild Atlantic salmon during this past century has not been established. Unquestionably human impacts have been substantial and likely will continue to play an important role in the future. Sustainability of Atlantic salmon ecosystems may depend on continuous analysis of human impacts and the development of models that incorporate anthropogenic changes.

Atlantic salmon warrant special recognition for a number of reasons. The species has a significant cultural and economic value for which substantial public interest and support exists. Much is known about their biology. Because of the association between salmon and pristine natural environments and their low tolerance to environmental degradation, Atlantic salmon serve as a potential indicator of environmental quality over a range of environments. This species has an extensive natural range with a complex anadromous life cycle that provides a framework within which to integrate information across a variety of spatial and temporal scales. Finally, Atlantic salmon are part of a wider grouping of anadromous salmonid species that share many aspects of biology, ecology, and habitat demands. For these reasons, the Atlantic salmon ecosystem may be a model system for examining how human development interfaces with conservation and how meteorology, ecology, sociology, and policy can be integrated to achieve a common conservation goal.

This paper details threats to sustainability of wild Atlantic salmon and their ecosystems from projected increases in human population growth and suggests strategies to ensure the persistence of this species. Specifically, we model how we might anticipate general trends and proactively influence anthropogenic changes using a conceptual framework that relates climate, humans, and the Atlantic salmon ecosystem. First, we describe the functional role of each component of our model and how each relates to Atlantic salmon abundance, sources of human impacts, consequent trends, and the state of our knowledge. Second, we describe how the model works detailing interactions among components. Thus, our emphasis is on the relationship among model components rather than the quantitative output of the model. Finally, we make some recommendations for the persistence of Atlantic salmon, and, in so doing, suggest where biological science, sociological research, and systematic monitoring can help us address how to conserve resources in the face of continued human impacts.

Conceptual model of interactions among climate, the human system, and the natural ecosystem of the Atlantic salmon

Components of the model

General

.The goal of our model is to provide a schematic and conceptual framework for compartmentalizing the key factors that drive expected and unexpected change so that we can establish appropriate institutions and policies. The three major sectors of our conceptual model are climate, the human system, and the Atlantic salmon ecosystem (Fig. 1). Two subsystems exist within the human system, the social context and the control system (Fig. 1). Via four flow pathways, i.e., landscape alteration, direct use, external inputs, and resource competition, the human system impacts the Atlantic salmon ecosystem (Fig. 1). Three additional flows, i.e., food, ecosystem services, and quality of life, feed back from the Atlantic salmon ecosystem to the human system (Fig. 1). An appreciation of the impact and feedback mechanisms are critical to strategic planning. Herein, we seek to determine how human activity, development, and population growth affect the components of this model. Interactions between the human and salmon systems are adapted from a general model presented by Solecki et al. (1998).

Definition of model components: climate

Climatic conditions such as heat, pressure, wind, and moisture drive hydrologic and oceanographic conditions. Natural phenomena such as volcanoes and sunspots act as phenomenological drivers to alter climate. Via changes in temperature, rainfall, flooding, drought, or other flow alterations, effects of climate on Atlantic salmon and their ecosystem can be substantial (Fig. 1). Climatic effects on temperature can affect Atlantic salmon at all life stages, habitats, and seasons (Scarnecchia et al. 1989; Gudjonsson et al. 1995; Friedland 1998). Distributions of Atlantic salmon at sea are directly related to ocean climate and sea surface temperature (Scarnecchia 1984, Martin and Mitchell 1985, Reddin and Shearer 1987; Friedland 1998). Climatic effects related to rainfall also can severely affect salmon by causing flooding, drought, and flow alterations (Power 1981; Gibson and Myers 1988; Cunjak et al. 1998). Impacts of climatic conditions vary in both spatial and temporal scale from local/short-term to global/long-term. For example, localized flooding may alter sediment loads and routing within a section of stream whereas changes in weather patterns associated with volcanic activity are global and may vary from brief but severe El Niño events to warming or cooling occurring over centuries. Furthermore, decadal shifts in the distribution of sea surface temperatures (UNESCO 1992) have affected survival of Atlantic salmon (Friedland 1998).

Climatic change could impact Atlantic salmon in a number of ways. Changing climate could significantly alter general ocean circulation patterns with a resultant change in the spatial distribution of fish stocks (Laevastu 1993). Spatial and temporal changes in prey species may have severe implications (Henderson et al. 1992). Increasing temperatures may shift the geographic range of the salmon resulting in possible loss of more southerly populations (Bielak and Angus 1994). Fluctuating temperatures as a result of global warming may affect changes in sea-age at maturity as well as individual growth rates (Power 1981; Bielak and Angus 1994). Depending upon changes in patterns and quantities of rainfall, the freshwater environment available for juvenile salmon production would be augmented or reduced (Moore et al. 1997). Hence climate and climate changes can affect survival, growth, distribution, and persistence of Atlantic salmon.

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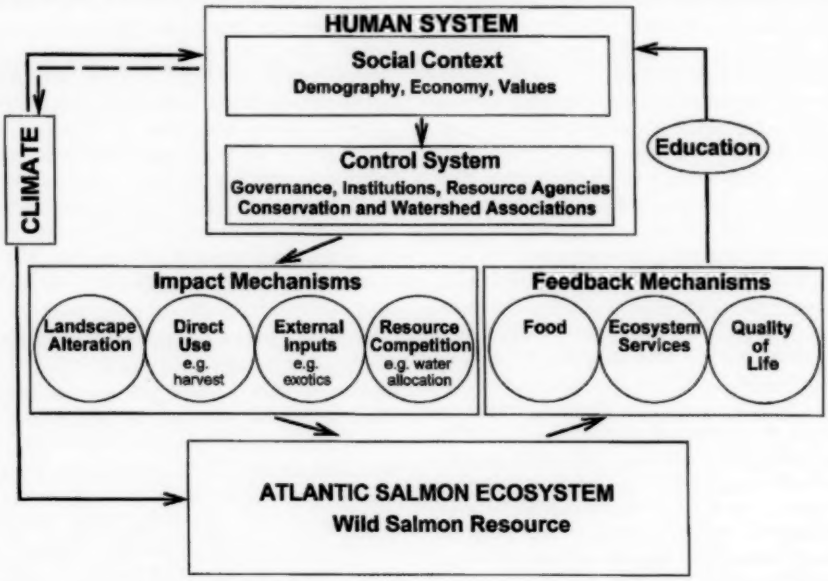
Fig. 1. Conceptual model of how climate, humans, and Atlantic salmon interact to anticipate change relative to human impacts. Climate, the human system, and the Atlantic salmon ecosystem, are sectors. The social context and control system are subsystems within the human sector. Impact and feedback mechanisms are flows. Education is a connector. Our ultimate goal is to positively influence the vigor of the wild salmon resource within the Atlantic salmon ecosystem. We argue that proactive change can be implemented by influencing the control system and through education of the value of an intact Atlantic salmon resource.



Definition of model components: the human system — social context

The next sector of the model, the human system, includes two subsystems, i.e., the social context and the control system (Fig. 1). Components of the social context which have the potential to alter the vigor of salmon populations are demography, e.g., population abundance, dispersion, age structure; economy; and cultural values (Fig. 1). Many scientists feel that other issues pale in comparison with the extent to which human population growth over the next 50 years will alter global resources (e.g., Brown 1996). The global human population is increasing by approximately 90 million people annually (World Resources Institute 1996). By the year 2040, the world population is projected to total about 9 billion people, representing a 57% increase from the estimated current population of 5.7 billion (Fig. 2*a*).

It is tempting to dismiss the threat of human population growth as insignificant to Atlantic salmon because much of the projected growth will occur in developing countries. However, the number of people using natural resources in the North Atlantic countries will also continue to increase largely due to immigration (Fig. 2*b*). Thus, pressure on resources will continue to intensify as both total energy of all forms (Fig. 2*c*) and specifically hydropower, a form of energy that especially impacts anadromous fish (Fig. 2*e*), continue to increase both worldwide and in North America and Europe. Hence Atlantic salmon likely will be profoundly affected by the demands of a growing population especially because per capita consumption of both total energy (Fig. 2*d*) and hydroelectric energy (Fig. 2*e*) by North America and Europe, the Atlantic salmon countries, dwarfs global trends.

Dispersion of the human population, another component of demography within the social context, can also affect Atlantic salmon by siting of cities near estuaries and rivers causing habitat loss, coastal erosion, and hydrological disruption (Fig. 1). In Europe, for example, over 20 of 55 European cities with more than 500 000 residents are in coastal areas (World Resources Institute 1996). In addition, in both Europe and North America, much of the population lives within the watersheds of large river systems, some of which contain Atlantic salmon. Because the demand for recreational fishing opportunities and the social and political framework within which fisheries are managed differ with population age distribution (Loomis and Ditton 1988; Murdock et al. 1996), changes in age structure, another component of the human social system, may also affect the Atlantic salmon ecosystem (Fig. 1). Although the world's population is growing at a rate of about 1.5% per year, the population over age 65 is increasing at an annual rate of 2.7% (World Resources Institute 1996). This age group may increasingly demand recreational opportunity or otherwise alter the social and political framework that manages the salmon resource.

Economic growth and the sources of economic support for the human system are also components of the human social system that affect the demands placed on natural resources (Fig. 1). As the population has doubled since mid-century, the global economy has nearly quintupled in size (Brown 1996). Increasing numbers of collisions between economic

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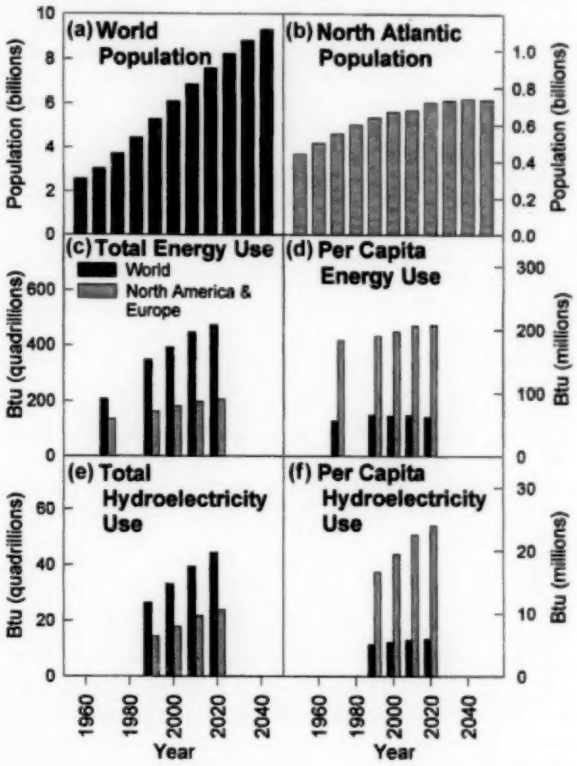
Fig. 2. Projected trends in (*a*) World population, (*b*) North Atlantic population, (*c*) Total use of all forms of energy, (*d*) Per capita use of all forms of energy, (*e*) Total hydroelectricity use, and (*f*) Per capita hydroelectricity use for the world and North American from 1960 through 2040. Population data were obtained from the 1996 U.S. Bureau of the Census International Database. For population, North Atlantic countries include Belgium, Canada, Denmark, Finland, France, Greenland, Iceland, Ireland, Netherlands, Norway, Portugal, Russia, Spain, Sweden, United Kingdom, United States. Energy data were taken from the 1996 International Energy Outlook, U.S. Department of Energy.



demands and the sustainable limits of fisheries, forestry, freshwater, and other resources have caused crises for many governments. Thus economics likely will affect all natural resources including salmon as the social context continues to change. Finally, cultural values play an overwhelming role in driving the impact that humans have on natural resources because they drive political and institutional policy (Fig. 1; Smith and Steel 1997). A large part of the failure to adequately protect salmon derives from institutional failure to recognize and specifically address the divergent interests and underlying values of their constituencies (NRC 1996).

Definition of model components: the human control system

Interactions between the human social structure and mechanisms that impact Atlantic salmon are regulated by an institutional infrastructure referred to as the control system (Fig. 1). This anthropogenic driver of change includes political and social entities through which natural resources are managed, exploited, or indirectly altered. Key elements of the human control system may include governance regimes of the countries that produce and harvest salmon, the agencies that have been established to manage natural resources, regional jurisdictional units that control water use, and local watershed and conservation boards that influence planning, development, and zoning. Cultural values ultimately drive decisions made by political and institutional entities, including public demand for species diversity, establishment of municipal green belts, parks, support for progressive resource management, and some forms of restrictive land use policies. Relative to the control system, a central problem for the protection of Atlantic salmon is that, like Pacific salmon (*Oncorhynchus* spp.), these fish are a "wide-ranging common-pool resource" (R.G. Lee 1997) and are clearly subject to the "tragedy of the commons" (Hardin 1977). The vast area used by even a single population as it completes freshwater and marine stages in its life cycle encompasses the jurisdictional boundaries of many institutions and governance systems. Effective protection of Atlantic salmon vigor will require integrating and coordinating among control systems to match the relevant spatial and temporal scales throughout the salmon life cycle. Control that is effected at local level of governance is likely to maximize positive feedback provided by human society from the salmon system because successful stewardship requires a myriad of small-scale institutions and land water users (R.G. Lee 1997). In addition, oversight at national and international levels will help ensure that broad scale environmental requirements of salmon are met.

Definition of model components: the natural Atlantic salmon ecosystem

Because of the complex life history and extensive migration undertaken by Atlantic salmon, its natural ecosystem is vast, including headwater streams and rivers in North America and Europe, their estuaries, and the North Atlantic Ocean in a range that extends for thousands of kilometres. A complex set of abiotic and biotic processes interact to determine the distribution, abundance, and persistence of the wild Atlantic salmon resource. For example, geomorphology of lotic systems may impact regionwide salmon patterns (Elliott et al. 1998). Across populations, many ecological and population parameters are correlated with physical variables (Power 1981). For example, abiotic factors such as temperature can affect egg-to-fry survival (Chadwick 1982), summer parr survival (McCrimmon 1954), overwinter parr survival and growth (Power 1981; Gibson and Myers 1988; Cunjak et al. 1998), the parr–smolt transformation (Staurnes et al. 1994), timing of smolt migration (Fried et al. 1978; Jonsson and Rudd-Hansen 1985), and grilse returns (Martin and Mitchell 1985). Depth, current velocity, and substrate determine juvenile salmon microhabitat use in summer (Morantz et al. 1987), fall (Gibson 1978; Rimmer et al. 1983, 1984), and winter (Cunjak 1988, Cunjak et al. 1998) across size- and age-classes (Symons and Heland 1978; Rimmer et al. 1984; DeGraaf and Bain 1986). Biotic interactions also influence the Atlantic salmon resources. For example, juvenile Atlantic salmon may compete between year-classes (Symons and Heland 1978), with other salmonid species (Hearn

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and Kynard 1986; Fausch 1998), and with other stream fishes (Symons 1976). Differential patterns of secondary production may influence these patterns of Atlantic salmon interactions (Poff and Huryn 1998). Predation can affect all life stages of salmon (Mather 1998) especially fry, parr (McCrimmon 1954), and smolts (Gunnerod et al. 1988). In addition, Atlantic salmon exhibit great within-population variability in life history traits (Saunders and Schom 1985; Hutchings 1998; Marschall et al. 1998) and population-specific differences in density, production, and growth rate occur (Grant et al. 1998; Kocik and Ferreri 1998). These abiotic, biotic, population, and community components of Atlantic salmon ecosystem are all susceptible to change associated with human impacts.

Long-term sustainability of the wild salmon resource in an increasingly human-dominated landscape will require maintaining diversity of gene pools and population structures (NRC 1996; Stouder et al. 1997) because genetic diversity is critical in providing evolutionary flexibility in response to an uncertain future. The network structure of local populations, that is, the metapopulation, confers a balance between this flexibility and local adaptation (Nielsen 1998). With the contraction that has been observed in the historic range of Atlantic salmon, particularly at its southern extremity, and extirpation of numerous runs, a substantial amount of genetic and structural diversity has been lost (Nielsen 1998). While scientists can provide estimates of population and genetic diversity required for continued viability at a given level of risk and the measures that may be required to attain this, decisions about desired probabilities of survival or extinction of Atlantic salmon, as well as the bearing of costs to do so, rest with society-at-large.

Impact mechanisms

Via planning, zoning, regulations, and laws, implemented at local, regional, national, or international levels, the control system of the human ecosystem directly influences the impact that anthropogenic change has on the Atlantic salmon ecosystem via four mechanisms. These anthropogenic drivers include (1) landscape alteration, the conversion of land from its natural state to human uses; (2) direct use of natural resources of the system through commercial exploitation or recreational harvest; (3) the addition of external inputs such as nutrients, pollutants, cultured or exotic organisms; and (4) competition between the humans and fish for resources such as water or forage fish.

Landscape alteration

Landscape alteration via the conversion of undisturbed watersheds to agricultural and urban uses removes habitats once accessible to salmon and degrades habitat quality (Fig. 1). Habitat is considered here to comprise both physical structure of the channel banks and bottom, water quality (e.g., temperature, dissolved oxygen, nutrients, environmental contaminants), flow properties, and the prey base (Mills 1989). Alteration of the landscape for agricultural production, urban residence, or commercial/industrial development can impact Atlantic salmon by altering the channel structure, adding organic and inorganic substances, and altering the water table, which can fragment the remaining habitats, set up barriers to movement, and alter flow (Table 1). Landscape alteration also modifies the riparian zone, which, in turn, affects the productivity of both Atlantic and Pacific salmon populations (Wilzbach 1985; Bilby and Bisson 1987; Gregory et al. 1987; Gregory et al. 1991; Gregory and Bisson 1997; Beschta 1997). Unwise forestry practices such as lack of buffer strips along streams and improper construction of roads and poorly sited and constructed bridges can be a serious threat to freshwater salmonid habitat. The extent of global modification of river and stream flows is staggering. For example, in Europe, the republics of the former Soviet Union, and North America north of Mexico, 77% of the total water discharge of the 139 largest river systems is affected by dams, reservoir construction, channelization, and interbasin diversion (Dynesius and Nilsson 1994). Furthermore, in the U.S. alone, 600 000 miles of previously free flowing waters are now impacted by dams (Escheverria et al. 1989). These and other hydrological alterations have major effects on magnitude and frequency of flow (Poff et al. 1997) as well as on geomorphologic responses (Petts 1984; Sear 1995).

All of these detrimental impacts of landscape alteration can result from agriculture, urbanization, or resource utilization. Impacts to salmon from landscape alteration as a result of agricultural activities will probably continue as the global human population grows. Agricultural production is increasing but the rate of growth is slowing (Brown 1996). Decline in the rate of food production is largely attributable to a decline in land area planted to grain, decreased fertilizer use, and little or no growth in irrigation water supplies as aquifers become depleted. Yet food demands of the growing human population are projected to increase by 64% globally and almost 100% in developing nations over the next 25 years (Harris 1995). Because most of the land suitable for agriculture is already exploited (Kendall and Pimentel 1994), increasing current food production likely will come from reclamation of marginal and ecologically sensitive lands and may further result in the loss of juvenile salmonid habitat. Intensifying the scale of farming practices could require increased fossil energy inputs of fertilizers, pesticides, and irrigation and may increase rates of soil erosion. Consequently, salmon streams could experience increased sedimentation and pollution from nutrients and pesticide and herbicide residues resulting in reduced survival of Atlantic salmon from egg to smolt (Mills 1989).

Landscape alteration that results from urbanization and other forms of development is likely to increase markedly with continued human population growth. By 2025, nearly two-thirds of the world's human population will be concentrated in urban environments (U.N. Population Division 1995). Atlantic salmon-producing countries are already largely urbanized, with more than 70% of the population in both Europe and North America living in cities or suburban areas (World Resources Institute 1996). Much of the shift in distribution will involve movement from concentrated urban centers to vast, sprawling metropolitan regions or to smaller-sized cities and will increase pressure on bordering rural lands with a consequent removal of forests, increased erosion, continuing sedimentation, thermal and nutrient pollution, and changes in the water table. Aquatic habitats in urban areas are often more highly altered than in any other land-use type (Booth 1991) and the increase in area of

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impermeable surface such as roads and roofs that are associated with urbanization leads to increased quantity and rate of surface runoff and decreased replenishment of underground aquifers. Further, domestic and industrial wastes that were historically deposited and degraded on the soil are now channeled into water bodies in immense volumes (Naiman et al. 1995). Increased industrialization associated with urbanization could lead to an increase in water abstraction, pollution (heavy metals, PCBs, endocrine disruptors, thermal), non-point pollution and novel pollutants of remote ecosystems (atmospheric pollution, acidification, greenhouse gases). Urbanization exerts disproportionate influences on salmon production because urban areas are frequently located in important migration corridors and wintering sites, and often in coastal areas (Gregory and Bisson 1997). Thus, human induced landscape alteration for agriculture, industry, and development that modifies the riparian zone and flow regimes can have major impacts on salmonids. Consequently, development related to these factors must be guided by expert biological advice in any conservation plan.

Direct use

Direct use of salmon ecosystems results from commercial and recreational harvest of Atlantic salmon throughout their geographical range (Fig. 1; Table 1). Some countries such as Spain and the United States restrict catch to a largely river-based recreational fishery while other countries allow both commercial and recreational harvest. Although some offshore fishing does occur, notably in the Baltic Sea, at present commercial harvest is generally centered in coastal and estuarine areas of Ireland, United Kingdom, France, Norway, Russia, the countries of the Baltic region, and Canada (Mills 1989). Overfishing has contributed to reductions in abundance of Atlantic salmon in many river systems throughout their natural range (Paloheimo and Elson 1974; Mills 1989). However, recent changes in regulations and quotas along with private buyouts of fishing quotas have greatly reduced interceptory fisheries in Canada, Greenland, and the Faeroes, and recreational fishing has become less harvest oriented (Rochon 1994; Vigfusson 1994, Windsor 1994).

Historical overexploitation does not preclude recovery of salmon populations if freshwater habitat is maintained in good condition (Mundy 1996) because, at least for Pacific salmon, sources of salmon mortality from habitat loss and degradation together usually exceeds fishing mortality (NRC 1996). Harvest regulation is a mainstay of many salmon management programs, and under current fishing regulations, Atlantic salmon catches are regulated by quotas based on forecast models. However, fishery harvest management will be insufficient to protect salmon vigor in the absence of habitat protection (Mundy 1996). Because harvest management is not immune from political influence, future demands for easing quotas may increase fishing pressure directly on the Atlantic salmon resource. In addition, increased numbers of hatchery and ranched salmon reared for direct utilization likely will also harm the wild salmon resource (Hansen 1994).

External inputs

Humans adversely impact freshwater, estuarine, and marine habitats of the natural Atlantic salmon ecosystem by the introduction of cultured salmon, exotic fishes, and other introduced aquatic organisms (Tarazona and Munoz 1995; Fig. 1; Table 1). Both supplementally stocked hatchery fish and by-products (e.g., pathogens, inputs of pesticides and antifoulants) from intensive salmon aquaculture are detrimental to wild salmon (Youngson et al. 1998, Youngson and Verspoor 1998). Aquaculture of salmon is increasing dramatically (Fig. 3*a*). For example, in 1985, salmonid species, mainly rainbow trout, *O. mykiss* and Atlantic salmon, represented 40% of total aquaculture production (Shepherd 1988). Norway produced 68% of Atlantic salmon with other major producers including, U.K., Chile, Canada, Ireland, and U.S.A. From the 1980s onward, wild salmon stocks have been greatly outnumbered by salmon of hatchery origin (Shearer 1992, Gross 1998). In 1996, for example, the production of farmed Atlantic salmon was 450 394 t in the North Atlantic. This is 150 times the nominal catch. A two-fold increase in farmed salmon production is expected by the year 2000, with little change in relative distribution among species and countries involved (Dunn et al. 1989).

The intentional and unplanned introduction of cultured salmon and exotic aquatic species has a number of threatening implications for Atlantic salmon (Table 1). Escaped hatchery salmon may affect the reproductive success of wild fish by altering their behavior, competing for resources, predation, spreading infectious diseases, interbreeding, and reducing genetic diversity (Table 1, ICES J. Mar. Sci. 1997). In addition, aquaculture reduces water quality via increased sediments, chemicals, reduced oxygen, and addition of antibiotics, antibacterial drugs, organophosphate pesticides, and anti-foulants (Table 1). The risks of disease outbreaks such as the M74 syndrome in wild populations of salmon are greater in areas of salmon aquaculture, where the effects may be compounded by large concentrations of salmon, reduced resistance, and localized increases in pollution incidences. The intentional or unplanned introduction of exotic aquatic species into freshwater, estuarine, and marine systems also impacts wild Atlantic salmon and other aquatic resources via many of the same mechanisms (Table 1). The migration of species into new habitats has always been a part of evolutionary processes but human activity has greatly accelerated the rate at which this occurs and represents a global phenomenon (Bright 1996). Although many exotic organisms fail to become established, the damage done by the small percentage that do has large ecological and economic consequences and the effects are largely unpredictable (Nitecki 1981). Especially in unconfined aquatic systems where unwanted organisms can escape control by finding refuges elsewhere, the consequences of exotic invasions are, almost without exception, irreversible (Naiman et al. 1995). Overall the impact on wild salmon populations of hatchery stocking, aquacultural operations, and exotic introductions can be displacement, declines, and even extirpation.

Resource competition

The fourth mechanism by which humans can impact the natural Atlantic salmon ecosystem is competition for limiting resources (Fig. 1; Table 1). A severe threat to salmon stems from competition with humans for water. Despite improvements in the efficiency of water use in many developed countries, human demand for freshwater for industrial,

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Table 1. Activities, mechanisms, and consequences of impacts to the Atlantic salmon ecosystem from the human system.

Activity	Mechanism(s)	Consequences	References
Landscape alteration	Altered channel structure and riparian zone through removal of riparian canopy, anchoring materials, and large woody debris habitat	Degraded habitat quality, resulting in dimished habitat carrying capacity, reduced salmon growth and survival	Wilzbach 1985; Bilby and Bisson 1987; Booth 1991; Gregory et al. 1991; Naiman et al. 1995; NRC 1996; Beschta 1997; Gregory and Bisson 1997; Pimental et al. 1997; Stouder et al. 1997
	Altered quantity and nature of organic, inorganic, and nutrient inputs to river as a result of agricultural activities, including forestry and mining, or in association with urbanization	Degraded water quality from sedimentation and pollution, resulting in reduced salmon growth and survival	
	Changes in water table and decreased replenishment of underground aquifers as area of inpermeable surfaces (e.g., roads, rooftops) increases	Loss of freshwater habitat, resulting in diminished habitat carrying capacity, reduced salmon growth and survival	
Direct utilization	Commercial and recreational fishing of salmon and other aquatic resources	Depletion and possible loss of some populations, altered age/size structure of populations, life history characteristics, and genetic composition	Paloheimo and Elson 1974; Rochon 1994; Mills 1989
	Recreational use of estuarine and riverine habitat		
External inputs	Stocking natural water bodies with cultured salmon; pollution from aquacultural facilties and operations		Horsbverg et al. 1989; Meyer and Schnick 1989; Bjorklund et al. 1990; Hindar et al. 1991; Iwama 1991; Lewis and Metaxas 1991; Craig 1992; Michel and Alderman 1992; Busack and Currens 1995; Sheridan 1995; Tarazona and Munoz 1995; Kapucinski 1996; Schnick et al. 1986; Youngson and Verspoor 1998
	Introduction of exotic fishes and other organisms		Nitecki 1981; Courtenay and Stauffer 1984; Bright 1996
Resource competition	Extraction of water from freshwater sources; channel and interbasin diversion; disruption of natural hydrologic regime from impoundments, wetland draining, channelization; degradation of water quality from pollution	Habitat fragmentation impedes salmon migration; displacement, declines in abundance, and possible extirpation of affected populations resulting from habitat loss and impairment of water quality	Petts 1984; Escheverria et al. 1989; Chisolm 1990; Gore 1992; Gleick 1993; Dynesius and Nilsson 1994; Naiman et al. 1995; Sear 1995; World Resources Institute 1996; Pimental et al. 1997
	Industrial fisheries	Reduced forage fish available to salmon resulting in diminished growth and survival	

agricultural, domestic, and leisure use has escalated with population and economic growth (World Resources Institute 1996; Postel 1996; Pimental et al. 1997; Fig. 3). In the last 50 years, withdrawals of freshwater from rivers, lakes, aquifers, and other sources have increased by more than a factor of four (Gleick 1993). At the same time, pollution has seriously degraded water quality and effectively decreased the supply of fresh water. Demands for clean water, recreation, and fish products are now doubling every one to two decades (Gore 1992; Naiman et al. 1995). To meet human demand, further extraction of water from rivers and lakes and other freshwater sources can be expected, resulting in continuing disruption of natural hydrologic regimes via interbasin transfers, impoundments, wetland draining, and channelization. Thus, Atlantic salmon, which need substantial instream flow and unimpeded up- and downstream passage, are likely to continue to compete for freshwater supplies not only with local human residents but increasingly with human populations that are distant from the freshwater source (Chisholm 1990). In addition, industrial

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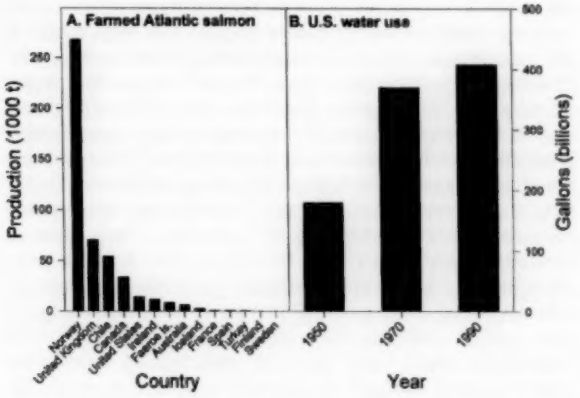
Fig. 3. A. World production of cultured Atlantic salmon in 1995 (FAO 1997; Gross 1998) and U.S. total offstream water use from 1950 to 1990 (U.S. Census 1997).



fisheries for forage fish such as capelin and sand lance are another example of potentially important direct competition between humans and Atlantic salmon for food resources, a trend that could contribute to the increased marine mortality of salmon (Table 1). Thus, resource competition by humans and fish for both water and food, if unregulated, has damaging effects on the Atlantic salmon resource. For conservation, development related to these impacts needs to be guided.

Feedback mechanisms

Benefits from the wild salmon resource feedback into the social context of the human system (Fig. 1), which, in turn, drives the control system to regulate the level and intensity of impact that human activities have on the sustainability of the wild Atlantic salmon resource. Three different flows feed back from the Atlantic salmon ecosystem to the human system: (1) supply of salmon and other aquatic resources as food, (2) provision of ecosystem services, and (3) enhancement of the quality of life (Fig. 1).

Food. Atlantic salmon and other aquatic organisms have long provided food for humans. However, today virtually all of the Atlantic salmon presently consumed by humans are produced by aquaculture. Presently, marine fish and shellfish from natural harvest and aquaculture provide nearly 6% of the world's protein and 16% of animal protein intake (Weber 1994). Although the situation is rapidly changing, the fishing industry still provides employment for 200 million people worldwide. The flow of food from the Atlantic salmon ecosystem to the human sector, however, could be a negative feedback loop that may diminish sustainability of the salmon resource (Fig. 4). Increased demand by the human system for fish protein is likely to lead to increased harvest of salmon, which may further diminish wild stock abundance. Pressure to meet demand may lead to increased stocking of hatchery fish, which could result in further decreases in the supply of wild salmon (Fig. 4).

Ecosystem services. The ecosystem that supports Atlantic salmon, when healthy, also provides for other basic human needs apart from production of food. These ecosystem services include the regulation of hydrologic cycles, absorption and detoxification of environmental contaminants, storage and cycling of nutrients, and moderation of climate extremes. Education about the role that these ecosystem services play is critical for the formation of a positive feedback loop in which public appreciation of the value of an intact system could lead to support for legislation to minimize deleterious human impacts and therefore protect and enhance the vigor of the salmon resource (Fig. 5).

Enhancing the quality of life. Atlantic salmon and their natural ecosystems also feed back to the human system in a third way by enhancing the quality of life and providing recreational opportunities and scenic attractions in the form of pristine aquatic habitats (Fig. 1). These benefits are likely to become more valued by an increasingly older and more urban society. Also included in this type of feedback are the assets associated with satisfaction of an ethical imperative to live in harmony with nature. Recent survey results of U.S. residents regarding their support for protection and restoration of salmon populations have shown that this imperative is surprisingly strong, particularly among younger, urban, female respondents, and among those who participate in outdoor recreation (Smith and Steel 1997). Like the provisioning of ecosystem services, this quality of life feedback is also a positive one (Fig. 5). Appreciation of the quality of life that an intact healthy Atlantic salmon ecosystem provides is likely to lead to public support for legislation that leads to its protection (Fig. 5).

Model function

Interactions among components

We ultimately seek to maximize the vigor and abundance of the wild salmon resource within the Atlantic salmon ecosystem (Fig. 1). In our model, the first sector, climate, influences both the human system and the Atlantic salmon ecosystem (Fig. 1). In turn, concern is mounting about the reciprocal effect that humans are exerting on global climate. Specifically, recent advances in the detection of global climate change indicate that "a pattern of climatic response to human activities is identifiable in the climatological record" (IPCC 1995). The emission of greenhouse gases is predicted to increase the global average temperature of the atmosphere by 2.5–4.5°C by the end of the 21st century. Realistically, though, we cannot control climate nor can we influence how this variable affects salmon. We can only monitor it and incorporate these trends into the model. The second sector in our model is the human system. The social context of the human system, i.e., human demography, economy, and values, is affected by the Atlantic salmon ecosystem through the three feedback mechanisms, food, ecosystem services, and quality of life, and can be additionally influenced by education, environmental awareness, and technology (Fig. 1). In turn, the social context drives laws and environmental protection regulations identified by governance regimes, legal institutions, resource management agencies, zoning boards, and conservation and watershed associations implemented in the control portion of the human system. The control structure of the human system via the same laws, policies, and regulations affects the salmon resource

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Fig. 4. Possible negative feedback from the supply of food (market salmon or other food resources) to the abundance of wild salmon. Discrepancies between human demand and supply may drive harvest which could diminish wild stock abundance. Continued demand could lead to supplementation of supply with hatchery fish which could further diminish wild stock abundance.

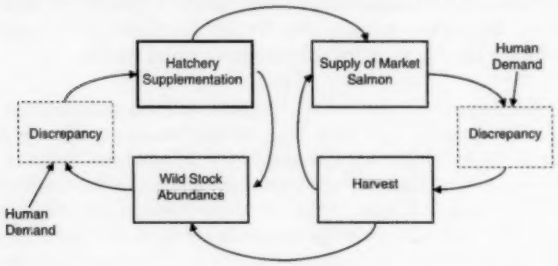
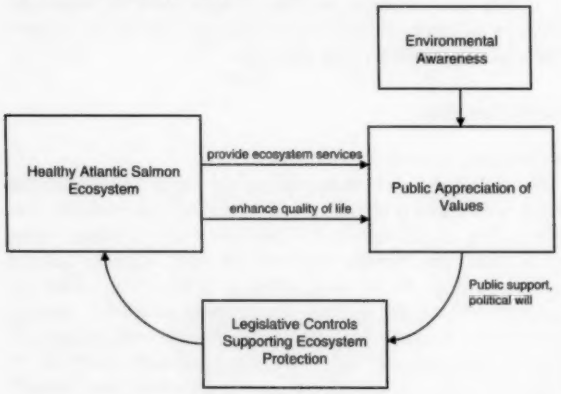


Fig. 5. Possible positive feedbacks from services provided by a healthy Atlantic salmon ecosystem. Environmental awareness leads to appreciation by the human sector of the values supplied by a healthy ecosystem in providing necessary ecosystem services and in enhancing the quality of life. This leads to public support and political will to mandate legislation control that support ecosystem protection by minimizing deleterious human impacts through restoration activities.



positively or negatively by landscape alteration, direct use, external inputs, and resource competition (Fig. 1).

Promoting greater public awareness of these feedbacks is critical to garnering the social support required to ensure continued persistence of salmon systems. Historically, economically driven interests to maximize the human food benefit of the salmon resource (food feedback mechanism in Fig. 1) have received greater attention from policy-makers than have more indirect ecological benefits such as ecosystem services or quality of life. Because scientists and resource managers can inform but not determine relative weighting of economic versus ecological values, protection requires the public to engage in a debate on how salmon and ecosystems fit into our economic and social vision (Smith and Steel 1997). Thus, biological and social research on change and anthropogenic impacts that promote environmentally friendly local governance structures within the control component of the human system will facilitate the conservation of Atlantic salmon.

An example

Is it possible to predict human impacts that may appear in the next two decades and can planning processes be implemented now to anticipate these changes? The answer is yes for major trends that have their roots in current cultures and maybe for trends associated with increasingly consumptive populations. Telecommuting is an example of one trend that could either sustain or degrade salmon populations. For example, as technological advances in computers and communications allow workers to be effective away from a centralized work place, telecommuting may become more prevalent. As a reasonably affluent population relocates to rural areas and develops small parcels of land, increased erosion, stream sedimentation, pollution, and general habitat degradation could result. In rural areas lacking a proactive control system, rampant uncontrolled growth may result, little information will be collected to document these changes, resource exploitation and land-use changes may be poorly regulated, and the salmon population will decline. In contrast, in a rural area with effective institutions and cultures, good planning and environmental awareness will exist, the ecosystem will be monitored, restoration and rehabilitation will be central features of exploitation and conservation policies, and the salmon population can be sustained. Thus, although we cannot stop human development, via an effect control system, we can influence development and population growth in a way that promotes conservation.

The effect of public interest and its underlying values in driving the control system cannot be overestimated. Numerous examples exist of "grass roots" initiatives leading to policy change and successful remedial preservation, restoration, and rehabilitation. When sportfish and wading bird populations declined as a result of U.S. Army Corps of Engineers channelization of the Kissimmee River, public rallying led to a legislative mandate to recouple 90 km of river with its floodplain in the largest river restoration project yet attempted (Koebel 1995). Citizenry rallying around the endangered species act to protect the spotted owl and certain populations of chinook and coho salmon caused changes in forest practices in the Pacific Northwest (U.S.A.; e.g., FEMAT 1993). In addition, citizen groups backed by academic institutions that provided data on water quality decline, successfully lobbied for construction of lake rim sewage collection systems to improve water quality in Lake Washington, WA, and Gull Lake, MI (Moss 1972; Edmondson 1977). Thus, humans can have positive and proactive input into the control system via governance and thereby can effect positive changes that will help conserve Atlantic salmon.

Recommendations for ensuring the persistence of Atlantic salmon

We have described some likely impacts on Atlantic salmon and their ecosystem from projected increases in human population growth and resource consumption to remind scientists and resource managers of the obstacles that will impede efforts to protect and preserve the wild salmon

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resource. A denser human population does not spell inevitable doom for Atlantic salmon, but reconciling the needs of the fish with those of humans will challenge the ability of scientists to produce needed data, communicate with the public, inform the regulatory process, and influence our control systems to respond appropriately and effectively. The latter will require public endorsement and political will. Some suggestions for improving the effectiveness of scientific efforts, closing the gap between management and science, and enhancing public endorsement through education follow. A specific recommendation for the establishment of an international salmon organization for research and guidance integrates these three areas.

Research needs — improving effectiveness of scientific efforts

Although Atlantic salmon have been well studied, our model has shown several critical gaps in our knowledge. Specifically, we need to better understand linkages among key variables and how these will respond to change and continued human impacts. Several lines of research can help provide this information. First, we need to monitor changes in the social context, i.e., demography, dispersion, economics, and values, and through integrated bio-social research seek to understand how these social variables influence the valuation of the Atlantic salmon resource. Second, because the control structure of the human system can affect the salmon resource positively or negatively, we need to understand through integrated interdisciplinary research what types of institutions, regulations, and policies lead to effective conservation and environmental protection. For example, behaviors of organized systems emerge that are not predictable based on individual behaviors (Bella 1997). Specifically, we need to identify what types of land management, harvest regimes, regulation of exotics, and water transfer protocols help both conserve the abundance and vigor of the Atlantic salmon resource and are palatable to the public.

Third, we need to understand what abiotic, biotic, population, and community, and ecosystem level variables influence Atlantic salmon distribution, abundance and persistence. Specific technical information relating to Atlantic salmon biology that is needed includes: (*a*) identification of nonlethal indicators that can serve as early warning signals of threats to the population i.e., smolt sex ratios, size at spawning; (*b*) quantification of stage- and environment-specific mortality rates across years and systems; (*c*) identification of metapopulations and evaluation of the extent of straying; (*d*) evaluation of the impact of hatchery success on productivity of wild salmon; (*e*) understanding of the effects of altered hydrology on life histories; (*f*) understanding of determinants of freshwater and marine habitat carrying capacity; and (*g*) information on the intensity and nature of linkages across marine, estuarine, and freshwater habitats. Fourth, we need to understand how changes in the feedback mechanisms, i.e., food, ecosystem services, quality of life will affect the social context, especially the human valuation of the salmon resource. Fifth, we need to know what types of education, rewards, and public awareness will increase public valuation of an intact salmon resource. Finally, our information gaps also reflect a need to expand the spatial and temporal scales of scientific studies to better match those of the salmon as well as to synthesize across broader spatial scales. Fully utilizing the capabilities of geographic information system (GIS) technologies to perceive and analyze spatial pattern can assist in this endeavor.

If we are to project general trends and encourage conservation-minded development, we must explicitly address sources and magnitude of uncertainty as well as the context in which this variability should be interpreted. A number of ways exist to deal with uncertainty. First, we can sample more effectively. Many fisheries studies lack a rigorous experimental design, and managers have faced controversy when results appear consistent with several alternative mechanisms or when results yield little information (McAllister and Peterman 1992). By using a precisely focused question, refined sampling design, increased replication within and across years, and placing greater emphasis on hypothetico-deductive inferencing processes (Irwin and Wigley 1993), we can reduce one level of uncertainty. Unfortunately real problems do not always lend themselves to replication and rigorous treatment-control comparisons and, in many cases, limited numbers of experimental systems or high costs will prevent adequate replication of ecosystem experiments (Carpenter 1989). In such cases, use of sophisticated statistical techniques with rigorous, focused hypothesis testing will be required to analyze data (e.g., BACI, Stewart-Oaten et al. 1986; RIA, Carpenter et al. 1994).

Expanded use of models to explore the dynamics of salmon ecosystems would assist in conceptualizing problems and in developing hypotheses that can guide research and monitoring studies. A number of techniques are available to improve model robustness. Techniques such as sensitivity analysis help to identify which parameters need to be identified most accurately and enable exploration of alternative management scenarios (e.g., Conroy et al. 1995). Error analysis, employing Monte Carlo simulation or simple first-order analytical techniques, allows evaluation of the effects of random error (e.g., Charles 1983; Bartell et al. 1986; Rossi et al. 1993; Carpenter et al. 1994).

Some degree of uncertainty is inherent in any complex problem. Uncertainty can be dealt with explicitly by either incorporating it directly into statistical decision models or acknowledging that unknowability is an inherent property of complex systems (Francis 1997). In addition to explicitly documenting and acknowledging uncertainty, ways are needed to effectively communicate this information in a framework that scientists, laypeople, and policy makers can understand. Specifically scientific advice needs to be expressed in probabilistic terms to convey uncertainty about the consequences of alternative policies (McAllister et al. 1994). Other disciplines have made a good start at this using decision theory and risk analysis and these principles are beginning to be applied to biological problems (Francis 1992; Caddy and McGarvey 1996; McDaniels et al. 1994). A research agenda for proactively dealing with change caused by human impacts should address all of these facets of dealing with uncertainty.

Dichotomies for philosophical approaches to science and management have been reviewed by Francis (1997), Botkin (1990), and Holling (1993). These dichotomies, which debate the value of reductionist vs. holistic research, are useful

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ways of identifying the components to think about the process. However, as working models, both the analytical/first stream and rational/sond stream approaches are oversimplifications. A hybrid approach is more realistic. This hybrid approach would recognize that explicit, technical information is needed to solve problems. In many cases the scientific method has worked well and provided valuable, technical biological information. This hybrid approach would also acknowledge that some degree of uncertainty exists in every problem, and that integration and synthesis are the ultimate goals of information gained through technical, reductionist approaches. For example, applied problem-solving, i.e., conservation and management, requires the integration of technical aspects of biology, social science, economics, an understanding of the role of values, and knowledge of how effective policy is made (Hughes 1997). This hybrid approach to research would utilize information from all methods that provide information about outcomes to different environmental scenarios. In addition, this hybrid philosophy would embrace the need for managers to act now, manage adaptively, and learn by deliberate experiment (K.N. Lee 1997) but would also acknowledge that trial and error will not provide useful information. Although management decisions need to made now with or without complete understanding, a research program that collects the right kind of information (Walters 1997) needs to instituted to improve the quality of information available for future decision making.

Thus, to effectively conserve natural resources like salmon, we need to track trends and set up institutions and cultures that can respond quickly to these trends in a way consistent with conservation. Projecting trends followed by consequent modification of projections based on available data is a viable option for dealing with change. An effective "human control system" that can respond to change with decisions about development that are consistent with conservation needs technical information from many disciplines collected in a rigorous, focused, way that moves beyond the mere description of how a single system behaves in a single year under a unique set of stressors.

Improving institutional response

In environmental science, the transfer of information from basic research to practitioners does not happen quickly. Criticisms are often leveled at basic researchers in academic institutions for being isolated and out of touch with real world issues and at resource managers and policy makers for being poorly informed. Establishment of a closer, collaborative relationship between researchers and resource managers would benefit each profession. Researchers would benefit in gaining access to management areas for use as experimental systems. Managers would benefit in gaining more rapid access to research results that could feed into adaptive management programs as well as in obtaining guidance in design of monitoring programs. An adaptive management approach, wherein management activities are conducted as experiments to test hypotheses and to develop information needs for future natural resource management (Hilborn 1987) will greatly enhance institutional response to changing conditions affecting salmon (e.g., Milliman et al. 1987; Walters et al. 1992).

Informing the public

Human society needs to be well informed about the benefits of an intact Atlantic salmon ecosystem before they can value it enough to institute laws, regulations, and policies that conserve populations and habitats via the "control system." Progress in protecting wild Atlantic salmon and their ecosystem hinges on gaining public support for this effort. Raising social awareness of the full range and extent of ecosystem services and benefits provided to society in maintaining a fully functioning salmon system can increase that support. Technology and information exchange can have a beneficial or harmful effect on interactions between the human and salmon ecosystem. For example, improved information exchange and technological advances have enabled development that both have hastened the degradation of salmon habitats and led to the use of renewable energy sources that minimize human impacts (e.g., Wichert 1995). Scientists have a vested interest in informing the public of environmental issues and environmentally compatible technological advances, and should avail themselves of every opportunity to do so.

Formation of an international Atlantic salmon forum

A multi-way exchange of information among scientists working in different countries is of paramount importance in increasing our understanding of interrelationships among natural environmental variation, human-induced changes, and salmon productivity. In a single-species context, some of these issues are addressed by scientific or administrative bodies that span national boundaries, e.g., International Council for the Exploration of the Sea (ICES), North Atlantic Salmon Conservation Organization (NASCO). There is an identifiable need, however, for an international research organization that considers environmental and management issues pertaining to salmon in a wider, multi-species research context. The mission of such an organization would include (*a*) sponsoring, promoting, and coordinating international research on salmon and their ecosystems, (*b*) providing guidance on how to monitor and integrate interdisciplinary trends in a way that would allow us to track, project, and interpret change. (*c*) providing a forum for exchange of information, (*e*) coordinating existing salmon research, (*f*) investigating new ways to interpret science for the public, (g) seeking innovative means to translate science into effective environmental policies, and (g) providing scientific guidance to policymakers of member countries relating to the maintenance and protection of salmon and their environments. This forum could work through multiple sites linked through the internet organized through an existing international organization such as NATO or UNESCO. To be effective, the forum should have a base budget that could facilitate staffing, a research program, educational outreach, and travel and meeting facilities for synthesis workshops among scientists, managers, and policymakers. With such a forum, positive feedback can be enhanced to stimulate the formation of environmental regulations and policy that will protect this valuable ecosystem.

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The application of science to the management of Atlantic salmon (*Salmo salar*): integration across scales

John D. Armstrong, James W.A. Grant, Harvey L. Forsgren, Kurt D. Fausch, Richard M. DeGraaf, Ian A. Fleming, Terry D. Prowse, and Isaac J. Schlosser

Abstract: The need for integration across spatial and temporal scales in applying science to the management of Atlantic salmon is considered. The factors that are currently believed to affect the production of anadromous adult Atlantic salmon (synthesized from recent reviews) are arranged in a hierarchy in which any given process overrides those processes at lower levels. There is not a good correlation between levels in the process hierarchy and levels in hierarchies of scale. This demonstrates the importance of integrating across scales in identifying the optimum foci for targeting management action. It is not possible to generalize on the need for integration across scales within management plans. This is because of the complex ecology of salmon, the broad range of characteristics of the systems of which they are a part, and the fact that both local scale and broad scale management can have broad scale effects. Many uncertainties remain regarding the large-scale components of the ecology of salmon, the way that small-scale mechanisms interact with life histories, and the way that different factors interact to limit production of fish. When more is understood of these processes, it is likely that generalized rules might be developed to predict the management requirements for stream systems. In the meantime, it is essential that there is good integration among managers working at different scales and it is important that management systems operating at all spatial scales include high-calibre expertise to compensate for the present paucity of general rules.

Résumé : On examine la nécessité d'une intégration suivant les échelles spatiales et temporelles dans les applications des résultats scientifiques à la gestion du saumon atlantique. Les facteurs qui, croit-on actuellement, influent sur la production du saumon atlantique anadrome adulte (selon une synthèse des études récentes) sont arrangés suivant une hiérarchie dans laquelle tout processus donné prévaut sur les processus des niveaux inférieurs. Il n'y a pas une bonne corrélation entre les niveaux dans la hiérarchie de processus et les niveaux dans les hiérarchies d'échelle. Cela montre l'importance d'une intégration suivant les échelles pour établir les cibles optimales des mesures de gestion. Il n'est pas possible de faire des généralisations en ce qui concerne la nécessité de l'intégration suivant les échelles dans les plans de gestion en raison de l'écologie complexe du saumon, du vaste éventail de caractéristiques des systèmes dont il fait partie et du fait que la gestion à l'échelle locale et la gestion à plus grande échelle peuvent toutes deux avoir des effets à grande échelle. Il existe encore de nombreuses incertitudes quant aux composantes à grande échelle de l'écologie du saumon, à la manière dont interagissent avec les cycles vitaux les mécanismes à petite échelle, et à la manière dont divers facteurs interagissent pour limiter la production de poisson. Quand on en saura davantage sur ces processus, on pourra probablement élaborer des règles générales pour prévoir les exigences en matière de gestion des systèmes fluviaux. Dans l'intervalle, il est essentiel qu'il existe une bonne intégration entre les gestionnaires qui travaillent à différentes échelles, et il est important que les systèmes de gestion fonctionnant à toutes les échelles spatiales soient assortis d'une grande expertise pour que soit compensé le manque actuel de règles générales.

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J.D. Armstrong. Freshwater Fisheries Laboratory, Faskally, Pitlochry, Perthshire, Scotland, PH16 5LB, U.K.
J.W.A. Grant. Department of Biology, Concordia University, 1455 de Maisonneuve Blvd. W., Montreal, QC H3G 1M8, Canada.
H.L. Forsgren. USDA Forest Service, P.O. Box 96090, Washington, DC 20090-6090, U.S.A.
K.D. Fausch. Department of Fishery and Wildlife Biology, Colorado State University, Ft. Collins, CO 80523, U.S.A.
R.M. DeGraaf. Northeast Forest Experimental Research Station, USDA Forest Service, University of Massachusetts, Holdsworth Hall, Amherst, MA 01003, U.S.A.
I.A. Fleming. Norwegian Institute of Nature Research, Tungasletta 2, N-7005 Trondheim, Norway.
T.D. Prowse. National Water Research Institute, Environment Canada, 11 Innovation Blvd., Saskatoon, SK S7N 3H5, Canada.
I.J. Schlosser. Department of Biology, University of North Dakota, P.O. Box 9019, Grand Forks, ND 58202, U.S.A.

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Introduction

This overview is one of a series of papers that consider integration across scales in relation to the biology of Atlantic salmon, *Salmo salar* L. The paper synthesizes the conclusions of other papers in the series, together with additional information, to evaluate the importance of integration across scales in applying scientific knowledge to the management of Atlantic salmon.

The two scales of physical and biological processes generally considered by ecologists are space and time. A fundamental characteristic of these scales is that when viewed as hierarchical continua, smaller-scale systems develop within the constraints set by the large-scale system (Rabeni and Sowa 1996; Lewis et al. 1996). Considering space and time as related to systems inhabited by salmonid fishes (e.g., Frissell et al. 1986), large scales, such as evolutionary time and catchment geomorphology, are at high levels of the hierarchy whereas small-scale processes, such as local sediment dynamics and development rates of individual fish, are at low levels.

Scale hierarchies have been viewed as useful models to focus aspects of the management of fish. For example, by applying scale hierarchies in the evaluation of the restoration of certain populations of fish in the Great Lakes, it was concluded that integration across scales is essential (Imhof et al. 1996; Lewis et al. 1996) and that large-scale processes should be considered preferentially in the first instance (Rabeni and Sowa 1996). A cautionary note was also sounded: that to recommend the management of large-scale processes may be arrogant because of ecosystem complexities and conflicts with other user groups (White 1996).

A main aim of this paper is to consider, for managing populations of Atlantic salmon, whether it is appropriate to focus on processes at any particular scale or whether it is appropriate to integrate across scales. If integration across scales is appropriate, then we aim also to establish what ranges of scales are most relevant and what might be the most suitable human resource structures for applying scientific principles to management over a range of scales. The paper comprises six parts in addition to the Introduction: (1) The general aims of managers of Atlantic salmon are outlined in relation to the general biological characteristics of the fish. (2) A general hierarchical structure relating the processes and factors that influence the numbers of salmon available to fisheries is developed. The principle of this *process hierarchy* is that processes at high levels override those at lower levels and so might be considered the preferred target for management action. The process hierarchy is constructed without reference to the scale hierarchies described earlier. (3) The process hierarchy is compared with scale hierarchies to ascertain whether there are good correlations between levels of processes and levels of spatial and temporal scales. If the correlation is good then, logically, it would be reasonable to conclude that management should, ideally, target the scales that correspond with processes high up the process hierarchy. (4) The extent of our knowledge of the biology of Atlantic salmon across the range of appropriate scales is assessed. (5) Drawing on the findings of the third and fourth sections, the scope for applying general science-based principles to the management of salmon is assessed. (6) The human organization framework needed to apply science to the management of Atlantic salmon effectively over the appropriate range of scales is considered.

A summary of management options

The requirements for management of Atlantic salmon depend on the life history (Hutchings 1998) of the fish. Salmon spawn in nests in fresh water. Young salmon ("alevins") emerge from the eggs and survive predominantly on a yolk-sac until they learn to feed on exogenous food (when they may be termed "fry"), which comprises mainly invertebrate larvae. As the salmon use up their yolk sacs and disperse from the redd they become known as "parr." They grow in fresh water for several years and may mature as parr. A proportion of the population, which may include previously mature and juvenile individual fish, is anadromous and changes from the freshwater form to the pelagic marine form (becoming "smolts") and migrates to sea during spring. Salmon may stay at sea from just over one year to several years before returning to fresh water to spawn.

The main management objectives in optimizing the success of fisheries are, first, to ensure that the numbers and quality of smolts produced by a spawning population, or spawning unit, of salmon are optimized. Secondly, to maximize the survival of smolts to adults. Thirdly, to regulate the proportions of adults caught by different fisheries and to ensure that a sufficient number of salmon returns to spawn. These management objectives might, in part, be attained by manipulating the chemical, physical and biological processes that affect salmon.

A hierarchy of processes affecting the production of anadromous adult salmon

The production of anadromous Atlantic salmon is influenced by a wide range of factors including chemical, physical, and biological processes. These processes and factors (which will be generically termed *processes* for convenience hereafter) can be arranged in a hierarchy of influence. Within this framework, processes on any given tier override those on lower tiers. The process hierarchy will vary between stocks of salmon, so here a general example is considered (Fig. 1) that includes many of the processes that affect many stocks in many rivers. The highest level processes are geology, climate, and those chemical changes that may influence geology and (or) climate. These processes may interact with one another. For example, change in chemical composition of the atmosphere, including perhaps anthropogenic oxidation of fossil fuels, may change global climate, while global climate, through its effect on temperature, may affect the need for humans to burn organic material. Geological processes, such as plate tectonic uplift and soil genesis, are critical in determining many physical characteristics of streams and rivers (Frissel et al. 1986).

The second tier includes geomorphology, determined by the interaction of geological processes and climate in the past. This basic "natural" feature influences two high-level anthropogenic processes: land use and introductions of fish species. In this context, land use includes a broad range of factors such as agriculture and in-river engineering works. Due to lag times, the climate that determined geomorphol-

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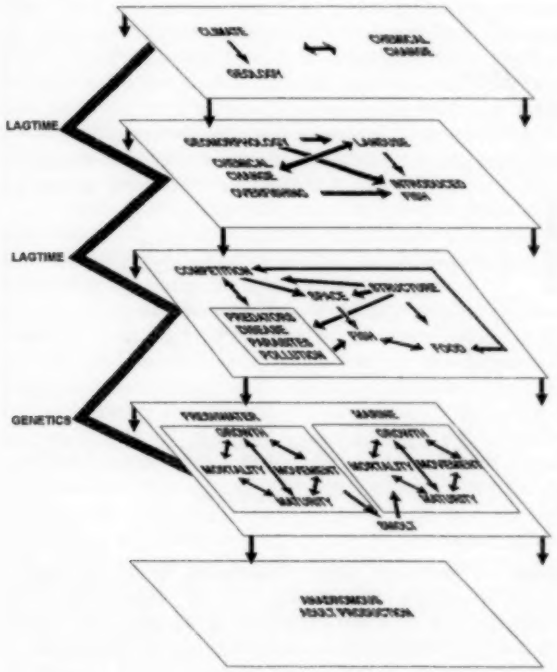
Fig. 1. A hierarchy of processes and factors affecting the production of anadromous Atlantic salmon. Processes on each tier override those processes on lower tiers. Arrows indicate interactions and move from the affecting factor to the effected factor. The processes on adjacent tiers may be linked by lagtimes and genetics (see text for details).



ogy might be quite different from that which now influences the way land is used. Similarly, lag times in the responses of river systems may result in rivers today being influenced by pollution and land use practices of past decades and millennia. Chemical changes, both "natural" and anthropogenic, that do not affect climate may be included on the second tier. The combination of processes on this tier within a stream or river catchment creates the environment for spawning and production of smolts. Similar principles apply in the oceans. Historically, geotectonics determined the positions of the continental masses and the forms of the ocean basins. Current climate determines the positions of the ocean fronts, which may affect the marine survival and growth of salmon (Friedland 1998). Ultimately, climate affects the distribution and abundance of non-salmonid fish stocks and this will influence the use of the sea by man and hence interactions between salmon populations and fisheries for other species. Geomorphology, through the development of inlets and fjords, underpins the distribution of introduced farmed salmonid fishes that interact with wild stocks of salmon (Gross 1998; Youngson and Verspoor 1998).

The third tier (Fig. 1) includes the fundamental local processes that affect individual salmon at any point in time. Many of the processes apply to spawning fish, juveniles growing in the river, and maturing salmon in the sea. Fish need suitable space (Allen 1969; Grant et al. 1998), may need suitable food (not in the case of eggs and returning adult fish), are affected by competitors (of the same and different species (Fausch 1998)), may be at risk from predation (Mather 1998), disease and parasites (Bakke and Harris 1998), and may be influenced by water quality. Spawning usually occurs only in areas of specific substrate and water flow conditions (Beland et al. 1982; Gibson 1993; Fleming 1996). As salmon fry and parr grow, their requirements change: they use deeper water, rougher substrate, and increased water velocities (Heggenes 1990). Habitat requirements may vary throughout the year, particularly in streams where ice cover is extensive in winter (Cunjak 1996).

The physical conditions available for spawning, rearing of juveniles, and survival of adults in rivers depend principally on geomorphology and the use of land in the river catchment, both by humans and the terrestrial communities of plants and animals. In addition to these factors, the aquatic community (including salmon, their predators, competitors, and prey) is affected by lagtimes such as occur with climatic influence. The fish faunas of many northern rivers remain impoverished in terms of species diversity following the last ice age so that there may be few species of fishes competing with salmon (Welcomme 1992; Wheeler and Maitland 1973). Artificial stocking can result in an acceleration of the process of recolonization and the introduction of non-native ("exotic") species of fishes. In effect, this may constitute anthropogenic manipulation of lagtime.

While the top three tiers include the factors that influence individual fish, the fourth tier includes the responses of fish to those processes. Local processes in the third tier can affect individual growth, mortality, age of maturation, tendency to move, and tendency to migrate to sea: these are the main components of life histories (Hutchings 1998). These responses may be interlinked since growth and mortality are often related (Beverton and Holt 1959) as are movement and maturity (Jonsson and Jonsson 1993) and growth and maturity (Metcalfe 1998). The scope within which salmon respond to any set of environmental circumstances is limited by their genetic constitution and so is influenced by past responses. In this way the genes of fish, together with the time for natural selection to occur, cause a lag in response. From the point of view of the management of salmon populations, the nature of the response at this fourth tier level is crucial since it determines the proportion of the population that migrates to sea and returns as the large adult fish of interest to fishermen.

Scales within the process hierarchy

Salmon occupy various ranges of scales of time and space at different stages of their life cycle (e.g., McCormick et al. 1998). Eggs are deposited within redds covering a few metres and incubate in a few months. Fry and young parr probably disperse for a period of weeks and over a range of the order of ca.1–1000 m. Parr occur within rivers for up to ca. 5 yr and during that time may range over a few metres to at least several kilometres (Erkinaro 1995). The smolt run occurs actively for several months and over most of the length of many rivers. Movements at sea may be over thousands of kilometres and over several years and the returning

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adults may stay within the river for over a year prior to spawning. When plotted together, the temporal and spatial scales encompassed by the salmon life cycle include a wide range of the possible combinations within broad limits (Fig. 2). In terms of space utilization, the salmon life history occupies a large proportion of the total scale. On the temporal scale, the life-cycle is short compared with the total extent of geological time. However, the processes of stock differentiation, the evolution of salmon and the influence of past climatic, geological, and anthropogenic processes (Fig. 1) extend the temporal scale considerably.

Since the third tier of the process hierarchy includes local processes and these are overridden by the processes in the top two tiers, it may appear that management should focus on large-scale processes. But this is not strictly true, because the top two tiers include some processes with immediate actions on local scales and others that act over large scales. Because anadromous salmon move over large distances, small-scale local processes may affect a large proportion of the population. For example, local pollution may affect every smolt leaving a river, and a single weir may impair every adult fish returning from sea. Because a large proportion of a salmon population may be clumped at certain times, for example when spawning in key local areas determined by geology of a river catchment, small-scale processes in those areas may severely affect the population. Large-scale processes may also, in some cases, have an overriding influence on salmon production. For example, human activities may cause widespread eutrophication, climate may result in a long summer growing season, and geology may result in a boulder-strewn river.

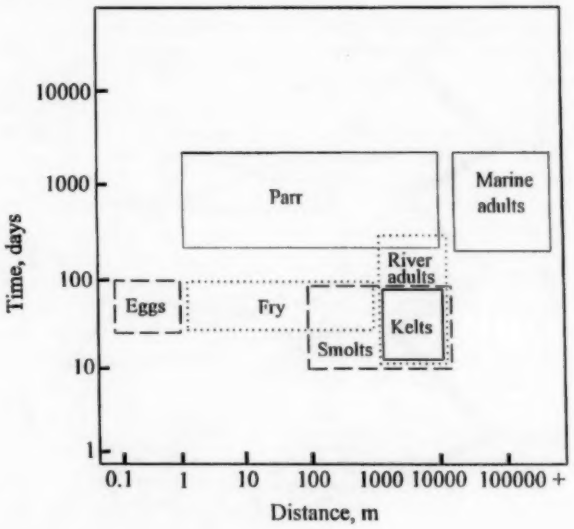
It is evident that factors operating over a wide range of scales may have influences on the survival and prosperity of an individual fish at any one point in time. For example, on the spatial scale, the abilities of salmon to utilize systems of olfactory cues may enable them both to home accurately as adults over thousands of kilometres (Quinn and Dittman 1992) and to manoeuvre as parr within a few centimetres in the stream to obtain the best feeding sites (Braithwaite et al. 1996). Hence, effects of pollutants on olfactory physiology may interfere with behavior and ecology over a broad range of scales. Temporally, at one extreme factors that influence evolution of the genome and geomorphological scales extend over thousands of years, while at the other extreme, the escape response of individual fish from predators operates at the scale of milliseconds. Both scales of process may effectively determine, at an instant, whether or not a salmon escapes from a predator, finds suitable cover, and survives.

Appreciating the large range of scales utilized and the vast areas of space that may be used during the lifetime of individual salmon is of fundamental importance for devising suitable research and management programmes.

Scale of research

In general, much is known of the small-scale processes whereas little is understood of the large-scale processes that influence production of salmon. To give some examples. While the nature and mechanisms of local site attachment are quite well understood (Stradmeyer and Thorpe 1987; Braithwaite et al. 1996; Armstrong et al. 1994, 1997) little is known of the mechanisms underlying large-scale movements of salmon parr (Gowan et al. 1994). Similarly, territoriality of emergent fry appears to be quite well understood (Gustaffson-Greenwood and Moring 1990) but there is little information on the extent and nature of fry dispersal in the wild. The nature of local movements of overwintering salmonids is becoming clearer (Heggenes et al. 1993), but little is known of the larger-scale movements that may be of overriding importance (Cunjak 1996; Cunjak et al. 1998). Consequently, it is difficult or impossible to model relationships between geomorphology, which determines the presence of special (and often limited) habitats that are crucial for spawning and perhaps over wintering, and the dynamics of populations. Very little is known of the biology of the movements of Atlantic salmon at the largest spatial scales during marine migration.

Fig. 2. Stages of the life cycle of Atlantic salmon in relation to scales of space and time. Kelts refers to the period during which adult anadromous salmon remain in the river after spawning; river adults refers to the period during which anadromous adult salmon are in the river prior to spawning; marine adults refers to the period when adult salmon are at sea.



Extrapolation to life history models of large-scale population processes from small-scale artificial systems should be cautious. Information on behavioral and physiological mechanisms underlying growth and maturity forms an important advance in our understanding of the mechanisms that may control life history processes (Metcalfe 1998), but we generally have little idea of how they act in nature. For example, direct links have been established between metabolic rate, early emergence, dominance, and age of smolting in cultured salmon (Metcalfe et al. 1995). However, it is not clear whether similar correlations apply consistently in natural streams where variations in dominance of fry early in life might act primarily to encourage dispersal from the redd. Behavior of salmon does not necessarily conform with the assumptions implicit in simple ecological models such as the Ideal Free Distribution (Armstrong et al. 1997). Therefore,

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more information is needed to understand how the distributions of salmon are influenced by the distributions of the resources they use and by interactions between individual fish.

Genetic responses constitute a lagtime between environmental conditions of the past and the present. As human influence on the environment results in rapid change, and manipulations of fish populations (for example by stocking) affect their gene pools, there is no certainty that populations are well-adapted to the habitats in which they live. This may greatly complicate the process of modelling the ecology of the fish since the normal null assumption that behavior is adapted to the local environment may be invalid. For example, the optimal response of salmon parr to de-watering appears to differ depending on whether it is to long-term drought or to short-term reduction in water flow (Armstrong et al. 1998). Hence, exposure of a population to a series of reductions in flow due to anthropogenic de-watering may reduce the ability of fish in subsequent generations to react appropriately to natural drought.

In general, our understanding of Atlantic salmon on small scales is increasing rapidly but we are only gradually expanding that understanding to encompass the larger-scale processes that impinge on the biology of the fish. This is being facilitated by the development of new techniques such as the application of miniature electronic tags for extending spatial scales of measurements (Prentice et al. 1990; Armstrong et al. 1996) and genetic tags (Nielsen 1998) for extending the temporal scale. Another advance in our knowledge arises from the continually increasing period over which natural populations of Atlantic salmon have been monitored. Given the many uncertainties in the base information available for developing policy, adaptive management, the process of monitoring current management policy to use it as a natural experiment (Lee 1993), is strongly advocated (Naiman et al. 1995). Failure to monitor the success or failure of management measures is a serious waste of an important opportunity to improve policy.

Application of science to management

From the preceding sections it is evident that in considering the application of science to management of Atlantic salmon it is necessary to integrate across scales. This conclusion is important because management processes, capabilities, and responsibilities may also vary across scales. For example, maintaining a local area that is crucial for salmon spawning may (in some countries) be within the powers of the local landowner, whereas controlling diffuse pollution may be the responsibility of a Government Agency. At a still larger scale, international organizations (NASCO and ICES) manage stocks of salmon on the high seas, which may include populations of fish from a number of different countries. Hence, to develop management plans that integrate the necessary management agents it is essential to understand what ranges of scales should be included. To be most effective, such plans should have general applicability so that simple protocols might form the basis for practical global policies. Unfortunately, the development of general guidelines for integrating across scales of management is confounded by the facts that river catchments that support Atlantic salmon are highly complex and vary greatly in size, and our understanding of the biology and ecology of the fish is incomplete.

This is illustrated by considering the management of smolt production. To increase the production of smolts in a river it is necessary to understand what is (are) the limiting factor(s). Cohorts may be limited by insufficient spawning fish, insufficient spawning areas, or a habitat bottleneck in the first summer after hatching (Armstrong 1997). During the development stage of parr there may be a limitation of space for foraging (Grant and Kramer 1990), refugia, or food (Poff and Huryn 1998). Over-winter there may be a bottleneck due either to inadequate habitat (Cunjak 1996; Mason 1978; Cunjak et al. 1998) or disproportionate mortality relative to growth (Armstrong 1997). Catastrophic or annual habitat changes such as drought (Elliott 1994) may limit cohort size. Other factors that occasionally or regularly may limit production of smolts are poor water quality, predators (Mather 1998), parasites, or disease (Bakke and Harris 1998). As well as influencing numbers of smolts produced, some environmental factors, such as temperature (McCormick et al. 1998), may influence the quality of those smolts and so the chances of their returning as adults to the fishery.

The various factors that may potentially limit the production of smolts relate to various scales. For example, food may be limiting due to the eutrophic state of the catchment (a large-scale process) whereas overwintering survival may be limiting due to the extent of suitable local refuges (which may be a relatively small-scale process). In some instances, large- and small-scale processes may be closely linked. For example, spawning activity may be limited to a few key areas (Schlosser and Angermeier 1995; Fleming 1998) that result from interactions between fluvial mechanics and the underlying geology. These areas may themselves vary in position over time as the river channel progressively moves. This presents an interesting interaction between scales: the large-scale process results in a need for careful management at a very local scale. There are still further scale implications for management strategies of such local "hot spots." Sampling effort should be deployed over a sufficiently broad scale at sufficient resolution to identify sites of key importance and at a sufficient spatial scale to monitor changes in their positions. Because the key factor(s) that limit the production of smolts may vary among river systems, or streams within a river system, it is not possible to derive one single overriding management action strategy.

A further potential problem of advocating generalized policies is the possibility of variations in the trade-offs between the multiple outcomes of a single policy. For example, a single catchment-scale policy, the encouragement of bankside vegetation, may have potential benefits, for example in stabilizing soils, but potential negative effects in accelerating growth rates of fish, through the introduction of invertebrate food, and by encouraging production of competitors of salmon, such as brown trout, *Salmo trutta* L. An increase in food supply produces only a modest increase in the standing stock of salmon; unfortunately, most of the increase in standing stock is caused by an increase in growth rate rather than an increase in the survival rate of parr (Grant et al. 1998). Consequently, depending on competition between cohorts, numbers of adults produced annually may not vary appreciably. In some instances changes in growth may lead to

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an increase in overwinter survival but may also result in increased incidence of maturity of male salmon as parr (Metcalfe 1998). This in turn may reduce the proportion of anadromous salmon since mature male salmon may have a high mortality and may stay in the river. There may also be a connection between slow growth and a tendency for salmon to return as multi-sea-winter fish early in the year (a resource of exceptionally high value in some countries) (Shearer 1990). If this connection is to some extent under environmental (rather than genetic) influence then modification of growth processes may have serious effects for fisheries. Finally, growth rates early in life may influence the numbers and sizes of eggs produced by anadromous adults (Jonsson et al. 1996).

The importance of choosing appropriate scales for studying population processes (Folt et al. 1998) can equally be applied to the consideration of such processes in management strategies. Management actions at a local scale can often make the most profound improvements to fisheries. For example, the removal of obstructions to upstream migrant salmon can open up large areas of catchments for the production of juveniles. Similarly, the removal of point sources of pollution may improve a large area of the catchment downstream. Salmon are particularly vulnerable as smolts leaving river systems. Damage by predators may be disproportionately intense at specific locations during the smolt run, for example, where fish are funnelled through hydroelectric-related structures. Hence, predator control policies (if pursued) should perhaps focus in the first instance at this small temporal and spatial scale.

At present there appear to be few simple and general rules relating the scales of the biology of salmon to management of the fish: each production system should be considered independently. In the past, much effort has been invested in the development of simple models (for some examples, see Fausch et al. 1988) that have not identified clearly the importance of hierarchical, rather than simultaneous, limiting factors. A clearer framework for relating scales of science and management may emerge in the future when greater emphasis is placed on classifying systems according to appropriate general characteristics, and then applying management models appropriate to the type. For example, it may emerge that models for predicting the abundance of parr are useful only in those rivers where spawning habitat is widely dispersed throughout the system. In this sense, a hierarchy of management priorities (e.g., first assess distribution of spawning areas, then apply the habitat model appropriate to the limiting factors) would be useful. Categorizing river systems and quantifying the scale of different impacting factors (Elliott et al. 1998) are important steps in rationalizing the management of salmon.

Promoting the application of science-based management concepts

We have focused on the identification of practical applications for the science-based concepts. However, we also recognize the difference between knowing how to apply concepts and actually getting them applied. Although there is much we do not know about Atlantic salmon, often more is known than is *used* to manage the species effectively.

If the application of science-based concepts in management of Atlantic salmon is to be increased, scientists will have to take an active role, as emphasized by Naiman et al. (1995). Figure 3 illustrates one model that summarizes an approach to maximizing the application of science in management decisions. This model suggests there are multiple paths that scientific findings may take to be adopted and used by managers. Several features are critical to the utility of the model.

First, at the foundation of the model, is an awareness on the part of scientists of the factors that motivate or are relevant to managers. The term "manager" is broadly used to describe the wide variety of individuals, groups, and organizations whose decisions affect Atlantic salmon. Managers therefore may range in scale from local land owners to international governmental organizations.

Sources of "motivation" are unique to different managers and are dynamic over time and (or) space. In general, people and organizations are motivated by those things that provide them value. Science that helps enhance management efficiency (e.g., reduce cost), increase management effectiveness (e.g., improve results), maintain or enhance management flexibility (e.g., options), meet legal or policy requirements, or ameliorate controversy is likely to be viewed as valuable, adopted, and used.

Second, the model requires explicit identification of relevant research findings and applications. This step is characterized as a "lens" in the diagram. The lens represents identification and consideration of the values, needs, and concerns of the intended audience. The lens is not in place to "muzzle" the scientist, modify research findings, or withhold "bad news." The purpose of passing the body of science through the lens is to focus and clarify the message — enhancing the utility of the information to the recipient or presenting the information in the context of the intended audience and therefore increasing the probability of its use. This active role is in contrast to the more traditional approach of completing research and expecting managers to discover its usefulness. The concept is also useful in the design of researchable questions that will be relevant to managers — but perhaps not as narrowly as management-directed research issues may sometimes be framed. Because "relevance" is dynamic, this sensing of values, needs, and concerns must be continuous.

Third, the model suggests the importance of making conscious decisions about who is best suited to convey the science information, fulfilling the role of credible liaison. Credibility is determined by the recipient of the information. In some cases this will be the scientists themselves. In other cases it will be an intermediary that is respected by both the scientists and the target audience. In still other situations, the most effective person to convey the information will be a peer from within the target audience. Credible liaisons are generally familiar with the target audience, can see the world through their "lens," and help promote understanding of that particular audience's values, needs, and concerns within the science community.

Finally, as noted previously, the model recognizes that scientific findings may become valuable to managers only after being relayed by other people or organizations that have influence with them. In the model these "relays" are

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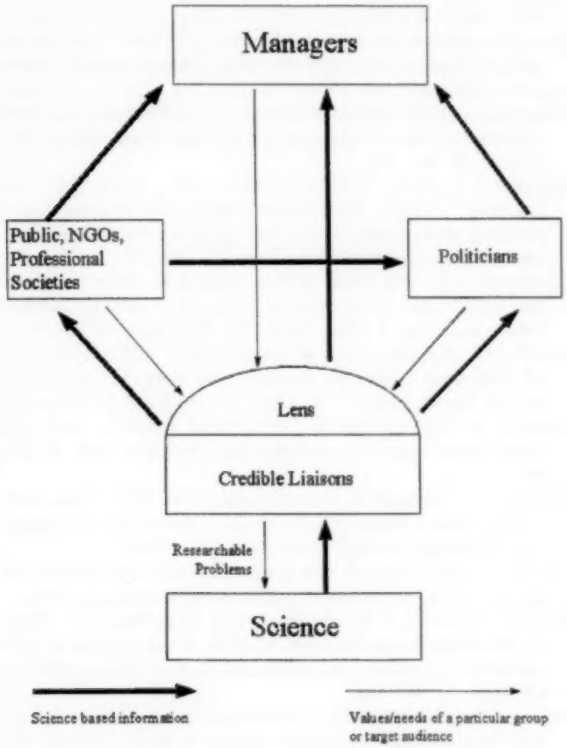
Fig. 3. A model of the relationships among science, managers of Atlantic salmon, and other interested groups of people. The ellipse represents a lens that focusses on values important to interest groups. NGOs is a term for non-government organizations.



represented by politicians, non-governmental organizations (e.g., conservation groups, sport/commercial fishing industry groups, professional societies), and the public at large.

Not evident in the diagram are other factors that contribute to the acceptance and use of science. In some cases the use of "best science information" is mandated by law (e.g., the United States' Endangered Species and National Environmental Policy Acts). More often than not use is facilitated by actions of enlightened scientists and managers, where effective working relationships are based on mutual respect, integrity, and honesty. Recognizing, communicating, and celebrating the benefits of successful application of science findings helps to reinforce and perpetuate the practice.

Concluding remarks

Hierarchies of scale can be useful concepts, when coupled with hierarchies of the processes that influence production, in developing strategies for managing Atlantic salmon. In broad terms, it is important to integrate across scales in considering the management of salmon. However, depending on what factor(s) limit(s) production on a particular system it may be appropriate to focus management actions at one particular scale or over limited ranges of scales.

Because of the complexities of the ecology of salmon and the geomorphology of river systems, there are not yet clear, unifying, science-based models available to managers. Instead, each river system should be considered independently. Consequently, it is essential that managers are well-educated and informed, have good analytical and observational abilities, and have a sufficiently high level of support facilities. Managers also need good access to scientific research that will provide new insights. Integration between managers operating at different scales (e.g., central Government and local land owner) is particularly important on those rivers where there is a need to consider a wide range of scales.

We have outlined some of the general requirements of managers of salmon, the general processes that impinge on production of anadromous salmon and some aspects of how science has started to provide critical information for supporting good management. We have also noted how our current understanding of the biology of salmon is inadequate and have highlighted some specific areas where a better understanding could usefully be developed. We have also noted that a first requirement for applying science to management is to focus on the key issues that may be considered to be priorities. To help focus the integration of studies of salmon at different scales on some of these key areas, we strongly advocate work to develop:

(1) estimates of the productive capacities of systems integrating realistic life history, fish behavior, and habitat models;
(2) a detailed understanding of where, when, and on what scale bottlenecks in production occur in different types of system and what the shortfall is between achieved production and the capacity of the system should successive bottlenecks be removed;
(3) realistic estimates of the capacity for and costs and benefits of manipulating systems to enhance salmon fisheries and conserve stocks.

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Elements in the development of conservation plans for Atlantic salmon (*Salmo salar*)

Julian J. Dodson, R. John Gibson, Richard A. Cunjak, Kevin D. Friedland, Carlos Garcia de Leaniz, Mart R. Gross, Robert Newbury, Jennifer L. Nielsen, Mary E. Power, and Steven Roy

Abstract: This paper examines two areas to be considered in developing conservation plans for Atlantic salmon (*Salmo salar*): goal statements and the general framework for the implementation of a conservation plan. From a biological perspective, the appropriate conservation unit for Atlantic salmon is the Evolutionary Significant Unit (ESU). As conservation decisions will rarely be based solely on biological information, the Operational Conservation Unit (OCU) is defined as resulting from the interplay between biological requirements and socio-economic issues. A multi-scale habitat inventory of Atlantic salmon rivers to know what their status is relative to historical conditions is the first step in a functional conservation plan. The viability of salmon populations may be assessed according to 6 variables: abundance, resilience, age and size structure, sex ratio, spatial and geographical distribution. A genetically viable population possesses the species' evolutionary legacy and the genetic variation on which future evolutionary potential depends. Four factors important to monitoring changes in a population's genetic health are genetic diversity, effective population size, genetic bottlenecks and founder effects and gene flow. Implementation of a conservation plan must be proactive to maintain the quality of the OCUs. Commercial and recreational fisheries need to be limited and several case studies are reviewed. The importance of avoiding the introduction of exotics and minimizing the impact of sampling methodology, as well as the pitfalls of planting eggs, fry, or parr, are addressed. Finally, the importance of fostering public awareness of the value of conservation is essential to apply the political pressure necessary to preserve natural resources.

Résumé : Cet article traite de deux éléments qui doivent être considérés dans l'élaboration des plans de conservation du saumon de l'Atlantique (*Salmo salar*) : l'énoncé des objectifs et le cadre général de mise en oeuvre du plan. Du point de vue biologique, l'unité de conservation appropriée pour le saumon atlantique est l'unité évolutionnaire significative. Comme les décisions en matière de conservation sont rarement fondées sur les seules données biologiques, on a aussi recours à la notion d'unité opérationnelle de conservation qui tient compte de l'interaction entre les exigences biologiques et les questions socio-économiques. La première étape d'un plan fonctionnel de conservation consiste à réaliser un inventaire à échelles multiples des habitats des rivières à saumon atlantique pour comparer l'état actuel des habitats à leur état passé. La viabilité des populations de saumon peut être évaluée en fonction de six variables : l'abondance, la résilience, la structure par âge et par taille, la proportion des sexes et la répartition spatiale et géographique. Une population génétiquement viable possède le patrimoine évolutionnaire de l'espèce et la variabilité génétique desquels dépend le potentiel évolutionnaire futur. La diversité génétique, la taille effective de la population, les goulots d'étranglement génétique et les effets génétiques du fondateur, et enfin le flux génétique sont quatre facteurs importants dans la surveillance des changements dans la santé génétique d'une population. La mise en oeuvre d'un plan de conservation doit être proactive pour assurer le maintien de la qualité des unités opérationnelles de conservation. Les pêches commerciales et récréatives doivent être limitées; à cet égard, on examine plusieurs études de cas. On traite de l'importance d'éviter l'introduction d'espèces exotiques et de minimiser l'impact de la méthode d'échantillonnage, de même que des problèmes liés à l'ensemencement au moyen d'oeufs, d'alevins ou de tacons. Enfin, il est essentiel de sensibiliser le public à la valeur de la conservation de façon à ce que puisse être appliquée la pression politique nécessaire à la préservation des ressources naturelles.

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J.J. Dodson. CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique), Département de biologie, Université Laval, Ste-Foy, QC G1K 7P4, Canada.
R.J. Gibson. 29 North Avenue, Mount Merrion, Co. Dublin, Ireland.
R.A. Cunjak. Biology Department, University of New Brunswick, Fredericton, NB E3B 6E1, Canada.
K.D. Friedland. National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, U.S.A.
C. Garcia de Leaniz. Servico de Monts, Rodrigues No. 5, Santandar 39071, Spain.
M.R. Gross. Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada.
R. Newbury. Newbury Hydraulics, P.O. 1173, 331 Headlands Rd., Gibson's Landing, BC V0N 1V0, Canada.
J.L. Nielsen. Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950-3094, U.S.A.
M.E. Power. University of California – Berkeley, Department of Integrative Biology, Berkeley, CA 94720, U.S.A.
S. Roy. USDA Forest Service, Federal Building, 151 West Street, P.O. Box 519, Rutland, VT 05701-0519, U.S.A.

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Introduction

Atlantic salmon (*Salmo salar*) conservation is inherently difficult due to the spatial and temporal complexity of the species' life history. Atlantic salmon migrate across freshwater, estuarine, and marine domains, freely crossing political boundaries within and outside their country of origin. They become the subject of land management issues, river resource usage, and allocation between competing fishing interests. Rearing habitats where salmon spawn and the young develop are often fragile habitats affected by pollution, forestry practices, and agriculture. In the marine environment salmon can undertake migrations that span most of the North Atlantic. They are frequently utilized in mixed stock fisheries, so nations must cooperate on harvest policies to ensure sufficient spawners return home. As such, conservation plans for Atlantic salmon are rarely developed by a single management entity, although some state agencies and river boards may develop their own plans. Putting cooperative plans in place is a daunting task, but there are a number of principals and important research areas that may be useful to consider in the making of these plans. This paper presents the results of the deliberation of a workshop panel formed to address the problems in developing a conservation plan for Atlantic salmon.

The panel recognized that the development of a conservation plan is a complex task that would require a broader cross-section of expertise than present on the panel. The panel also realized the investment required, in both time and resources, to learn the skills necessary to construct such plans. However, drawing upon the diverse expertise of the panel members, a number of ideas were developed which may be constructive for those interested in developing conservation plans for Atlantic salmon. This paper examines two general areas: the development and content of goal statements for conservation plans and the general framework for the implementation of a conservation plan. The elements under these subheadings are not intended to be a complete list, but rather, a collection of ideas and recommendations that planners might find useful.

Definitions

Four important terms related to conservation biology are defined according to Bradshaw (1996) and Fowler and Fowler (1971):

Restoration. The act of restoring to a former state or position, where the implication is of returning to an original state, one that is perfect and healthy.

Rehabilitation. The action of restoring to a previous condition or status. The term is similar to restoration except that there is no implication of perfection and no expectation of achieving the original state.

Enhancement. To raise or increase in price, value, importance or attractiveness.

Conservation. To maintain, protect, preserve or prevent from deterioration.

Rehabilitation and restoration incorporate the notions of time and change and have as an ultimate goal the recreation of some past condition. Thus, their reference point or target is sometime in the past. Enhancement implies improvement over the present situation. It may or may not take the original situation as the reference point. When enhancement seeks to improve by recreating past (supposedly better) conditions we are talking about restoration and rehabilitation (R&R) Thus, R&R is a particular subset of enhancement measures. However, enhancement may also consist in taking actions not necessarily aimed at restoring previous conditions. For example, the removal of a natural obstacle or the vaccination of fish against a natural disease are clearly not part of restoration and rehabilitation. Thus the reference (target) point of enhancement is either the past (R&R) or the future.

Conservation, protection, and preservation are synonymous terms. For clarity we will use the terms protection and preservation (P&P for short) and reserve conservation for the more general meaning of any plan aimed at maintaining ecosystems. Unlike R&R and enhancement, P&P does not aim to bring back past conditions, nor does it aim to create a future (hopefully better) state of affairs. P&P seeks to keep things the way they are, preventing further degradation, and thus anticipating future change. The reference point of P&P is the present. Thus, although all conservation plans are obviously projected into the future and have in common the notion of change, their target goals and scopes differ. In R&R, it is the past that is used as reference, in P&P it is the present, and in true enhancement it is the future.

Conservation goals

Adopting a unit of conservation

A critical issue in any conservation plan is to decide what to conserve. Some people might suggest that a conservation plan should save the species. However, we do not believe that the species is the appropriate conservation unit in the case of Atlantic salmon. First of all, the species is not threatened with extinction. In fact, there may be more Atlantic salmon alive than ever in history. The aquaculture industry alone produces over a hundred million Atlantic salmon, perhaps several times more than ever produced by nature (Gross 1998). Moreover, wild populations with many hundreds and thousands of free-swimming individuals can be found in at least some countries (e.g., Canada, Norway). Thus, the Atlantic salmon is not threatened as a species.

Instead, we suggest that a conservation plan must recognize that the Atlantic salmon species is composed of many evolutionary lineages whose survival is the issue for conservation. Because adult salmon migrate back to their natal spawning area and because these areas and migratory pathways may exert unique forces of natural selection, the Atlantic salmon gene pool has diversified into locally adapted units. The species is therefore a collection of unique populations with specialized adaptations (National Marine Fisheries Service 1995). These adaptations allow for viability within different stream habitats and may account for the broad geographic range occupied by the Atlantic salmon. Many of these populations are already extinct (e.g., much of the U.S.A. distribution) and others are vulnerable, threatened, or endangered. As the component parts are lost, so too is the species and its genetic heritage, part by part. Thus, the objective of a conservation plan for Atlantic salmon is to conserve its independent evolutionary lineages.

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The Evolutionarily Significant Unit (ESU)

From a biological perspective the appropriate conservation unit for Atlantic salmon is the Evolutionarily Significant Unit (ESU). Waples (1991, 1995) defines an ESU as a "population (or group of populations) that (1) is substantially reproductively isolated from other conspecific population units, and (2) represents an important component in the evolutionary legacy of the species." The concept thus incorporates both the genetic and ecological diversity of the species. Although the ESU concept was originally developed for Pacific salmon, it has been found to be appropriate for the biology of Atlantic salmon as well (National Marine Fisheries Service 1995). It also has the advantage of official recognition within the US Endangered Species Act (National Marine Fisheries Service 1991; US Fish and Wildlife Service 1996), probably Canada's developing act (Bill C-65), and perhaps other countries with conservation acts that recognize distinct populations (e.g., Spain). Thus, the ESU meets the need to conserve the component parts of Atlantic salmon and may also allow access to legislation that could ensure immediate conservation action.

Applying the ESU

Methods for identifying ESUs are described in Waples (1991, 1995) and the papers in Nielsen (1995). In brief, genetic and phenotypic data (morphology, physiology, behaviour, life history (egg size, age of maturity, etc.) are collected, where logistically feasible, from populations throughout the Atlantic salmon range. These data are analyzed by phenetic and preferably cladistic methods and the relationship(s) among populations are determined by hierarchical nesting (Vogler and DeSalle 1994). Populations that do not differ significantly from each other are grouped into a single ESU. Each ESU becomes a biologically-determined unit for conservation (Fig. 1).

Limitations of the ESU

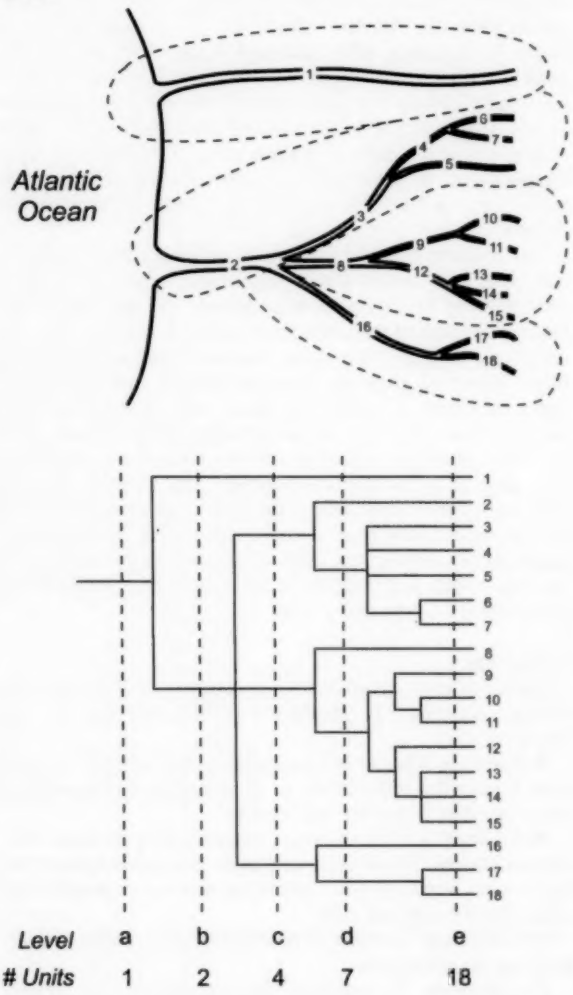
There is some controversy over the use of the ESU concept in conservation biology (see papers in Nielsen 1995). For example, there is no standard amount of significant difference among populations that is necessary to identify ESUs. As discussed by Waples (1995), a professional opinion must be applied in each case to the degree of difference that is deemed biologically significant.

Second, protecting ESUs is a "bottom-up" approach to conservation (Gross 1997). It identifies genetic and possibly ecological distinctions and ensures the protection of these. An alternative or "top-down" approach to conservation would place priority on preserving the ecosystem and assume that preservation of the ecosystem would also preserve the significant components of species. Waples (1995) points out that in order to preserve the ESU one must preserve the habitat on which it depends, thus by focusing on a definable unit one can work back up to the ecosystem.

Third, it is possible that not all distinctions between populations can be recognized by current measurement techniques. This would result in the grouping of populations of different lineages into a single ESU. Such grouping could result in the loss of the distinctions.

We recommend that the ESU be applied because it most clearly and effectively results in the preservation of genetic adaptations and the population structure required to maintain genetic diversity and the ongoing evolutionary process. In this way, the adaptations which allow survival in the present and the capacity for future adaptation through evolution are preserved for the Atlantic salmon.

Fig. 1. The two steps in identifying ESUs (adapted from Waples 1995: 24). First, one or more types of data are used to estimate evolutionary relationships among populations, as depicted here in a schematic diagram (top) and a phylogenetic tree (bottom). Second, a decision must be made regarding the appropriate hierarchical level on which to focus conservation efforts. For instance, a decision may be made to treat all 18 populations as conservation units (level e), or to recognize 7 units (level d), or 4 units (level c), or only 1 unit (level a). Here the decision is made to recognize 4 ESUs (distribution illustrated by dotted lines in upper panel). As all levels are consistent with the biological data, the final choice of hierarchical level may be influenced by social, economic and legal considerations. As such, the ESU becomes an Operational Conservation Unit (OCU).



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Socio-economic issues

Decisions about conservation will rarely be based solely on biological information. Social, ethical, legal, and economic issues will also determine the conservation effort. In many cultures, people are willing to place only a certain economic value on conservation while in others the economic resources simply do not exist for conservation (Loomis and White 1996; Moyle and Moyle 1995). Since the goal of most human-based conservation of biodiversity is to ensure resources for humans, social, ethical, legal, and economic issues (summarized for simplicity as socio-economic issues) will play a major role in deciding the operational conservation unit (OCU).

Operational conservation unit (OCU)

The OCU is the unit of conservation that results from the interplay between biological requirements and socio-economic issues. The biological requirements are largely found within the ESU. The OCU therefore reflects the ESU and its interaction with socio-economic issues. In some cases, sufficient economic resources and desire may exist within society to preserve all ESUs and thus the ESUs become the OCUs. In most cases, however, the OCUs may be larger units than individual ESUs, encompassing several ESUs into a single OCU. This may lead to the loss of biological capacity of the species, although this loss is presumably balanced by the needs of society. Thus, decisions about the OCU must weigh the socio-economic and biological trade-offs.

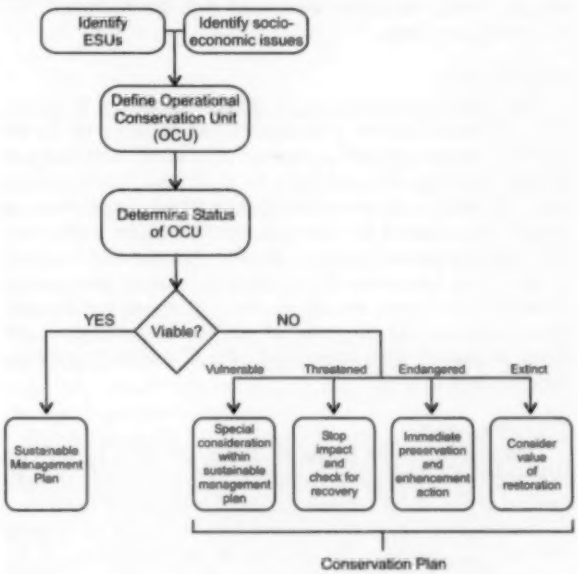
Applying the OCU

Developing a conservation plan for Atlantic salmon necessarily involves a series of stages. The first stage is to define the OCU. This is done through the identification of ESUs and socio-economic issues; through their mutual assessment by scientists, managers, and the public, a decision is made about the level of conservation (Fig. 2, and see below).

The second stage is to assess the status of the OCU (Fig. 2). Is it viable or not? Viability is determined through the genetic and ecological state of the OCU (see below), and also the existence of threats from human or other external activity to its habitat or individuals. For instance, the construction of a new pulp and paper mill within the ecosystem presents a habitat threat which must be taken into account in the assessment of the viability of the OCU.

If the OCU is found to be viable, a sustainable management plan is developed. This plan will allow harvesting without impacting the viability of the OCU. The management plan should be developed following the practices of "adaptive management" philosophy in which repeated trials are made under carefully observed conditions (Lichatowich et al. 1995). If the OCU is found not to be viable, it may be classified into one of several categories including vulnerable, threatened, endangered, or extinct, and an appropriate conservation action taken (Fig. 2). If vulnerable, the OCU should receive special consideration within a sustainable management plan. If threatened, current impacts should be immediately halted and the OCU checked for recovery. If endangered, immediate preservation and enhancement action is needed. Finally, if the OCU is extinct, then the value of restoration may be considered.

Fig. 2. The Operational Conservation Unit (OCU). The OCU is defined through the identification of ESUs and socio-economic issues. Viability is next determined through the genetic and ecological state of the OCU and also the existence of threats. If the OCU is found to be viable, a sustainable management plan is developed. This plan will allow harvesting without impacting the viability of the OCU. Alternately, the OCU may be found not to be viable. If classified vulnerable, the OCU should receive special consideration within a sustainable management plan. If threatened, current impacts should be immediately halted and the OCU checked for recovery. If endangered, immediate preservation and enhancement action is needed. If the OCU is extinct, then the value of restoration may be considered (from M. Gross, in preparation.)



OCUs and legislative boundaries

Protecting OCUs composed of stocks that migrate across boundaries to waters where they may be exploited or otherwise negatively affected without being legally recognized poses a problem to conserving a migratory species such as Atlantic salmon. The North Atlantic Salmon Conservation Organization (NASCO) is in the best position to implement policies on the protection of OCUs among its member states. NASCO's convention applies to the salmon stocks which migrate beyond areas of fisheries jurisdiction of the coastal states of the North Atlantic north of 36° latitude throughout their migratory range. Stocks that migrate through the waters of adjacent states would require specific protection under the fisheries jurisdiction of neighboring coastal states. Since the council of NASCO establishes working arrangements with the International Council for the Exploration of the Sea (ICES) and other appropriate fisheries and scientific organizations, NASCO is seemingly the appropriate organization to insure the protection of OCUs across legislative boundaries.

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Defining the value of the resource

The planning and application of a conservation plan is the result of perceived value associated with a resource (Riddell 1993; Scarnecchia 1988). Three values are defined that are commonly associated with a natural resource; biological, societal. and economic.

Biological value

This is the value associated with the unique genetic and ecological traits (adaptations) characterizing each ESU. Metapopulation structure that may involve several ESUs contributes to the maintenance of ecological stability and resilience as well as the evolutionary process. Conserving numerous ESUs allows life to continue in the face of future change. This is the value associated with the biological legacy of life on earth.

Societal value

This value is manifest in the desire to conserve in the absence of any monetary gain. Rather, the presence of the resource is associated with a sense of communal well-being or esthetic pleasure. For example, the traditional native American exploitation of some fish stocks whose importance in preserving a way of life through ceremony is far more valuable than the market worth of the fish; the restoration of degraded habitat uniquely for its esthetic value in increasingly urban environments; the conservation of nature for the purpose of retreat and the sense of well-being associated with being in contact with nature (e.g., the Biophilia hypothesis, Wilson 1984).

Economic value

This represents the financial returns obtained by directly exploiting the resource as a fishery, either for sport or commercial profit, or for the more general purposes of tourism.

The absolute value and relative importance of each value will vary according to the interests of the proponents of the conservation plan. In most cases, there may be conflict among resource users over the relative importance of each value. Furthermore, these categories are not necessarily mutually exclusive. An economic value may be applied to the first two categories by calculating the cash value forgone by not exploiting the resource for direct financial gain; alternatively, the biological legacy of life on earth may best be considered as priceless. The relative importance of each value must be determined in order to set the socio-economic stage on which OCUs are defined.

The functional plan

Assessment

Inventory of Atlantic salmon rivers and identification of keystone habitats

There is a need for a multi-scale habitat inventory of the Atlantic salmon rivers of the world in order to know what their status is relative to conditions prior to any major intervention/disruption to fish passage or habitat caused by human activities. The state to be measured and compared over time is the salmon potential of the river based on physical and biological habitat characteristics. If no biological data are available, relationships between habitats, river geometry, and drainage areas could provide preliminary information. Greater precision would be possible if detailed habitat information was available for stretches of river where change has occurred. Such comparisons between present and past conditions could guide the development of conservation priorities, as well as future restoration or rehabilitation programs. For example, by summarizing key physical parameters of present and historic salmon-bearing rivers (Table 1), the inventory could identify which rivers or river reaches would be most promising as habitat for re-introduced stocks. Other tabulated features, such as proximity to native wild salmon stocks, current catchment land use, and general ecological health would also bear on the potential of a river for rehabilitation as salmon habitat (as ranked in the last column of Table 1). Existing data bases could contribute to this effort; for example, the salmon rivers inventory maintained by NASCO.

At the within-river scale, salmon-bearing capacities of rivers depend in part on "keystone" habitats (Fig. 3). Although Atlantic salmon use a wide variety of stream habitats, there are certain critical, or keystone, habitats that strongly influence populations, either positively or negatively, that are great in proportion to the habitat's area. In the case of post-spawning adult salmon (kelts) for example, winter refugia from the potential effects of ice scour and accumulation, or from low stream flow, are often limited and best secured near the confluence of tributaries and main channels, behind islands, and especially in backwater channels (Komadina-Douthwright et al. 1997). Similarly, groundwater discharge zones and seeps often serve as thermal refugia during periods of high temperature stress (>23°C). Despite their very small areas, they are extremely important to heat-stressed salmonids.

There are general geomorphological relationships among rivers and within catchments that may permit identification of keystone habitats. The functional habitats of benthic insects and fish are related to the hydraulic conditions created by natural channel forms, for example in riffles, runs, meander bends, and scour pools. In some cases the preferred habitats coincide with the most frequently occurring hydraulic forms, suggesting that fish have adapted their behaviour to the natural geometry and behaviour of rivers (Newbury 1995).

A final consideration for restoration or rehabilitation projects is that the quality of habitat needed for re-introduced populations may be higher than the historical quality of rivers when they supported large salmon populations. Such "hystereses" could arise because of subtle effects. For example, large groups of spawning Pacific salmon coarsen the bed surface, reducing the probability of scour mortality for their young. If small numbers of salmon remain within a river system, for example, the size of gravels permitting successful reproduction may be more narrowly constrained.

Assessing population viability

(a) Demographic and ecological factors. Six variables that may be used to assess the viability, or health, of salmon populations. Healthy salmon populations exhibit the following characteristics.

Abundance. Healthy salmon populations exhibit recruitment levels sufficient to occupy all available habitat.

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Table 1. Habitat inventory of the Atlantic salmon rivers of the world. The inventory would summarize the present status of salmon rivers relative to their historic extent and condition. The difference between past and present state provides a measure of the scarcity of salmon habitat (percentage habitat remaining, for example). At a finer scale, variables such as the number and kind of keystone habitats, water quality, current catchment land use, stock status (ecological and genetic viability) and the proximity to native wild salmon stocks as a source of colonists would also bear on the potential of a river for rehabilitation as salmon habitat. An index of restoration potential could be developed from some combination of these variables.

Country/ river	Historical state	Present state	Scarcity	Keystone habitats	Water quality	Land use	Stock status	Proximity to source	Restoration potential
Country 1									
River 1									
River 2, etc.									
Country 2									
River 1									
River 2, etc.									
Etc.									

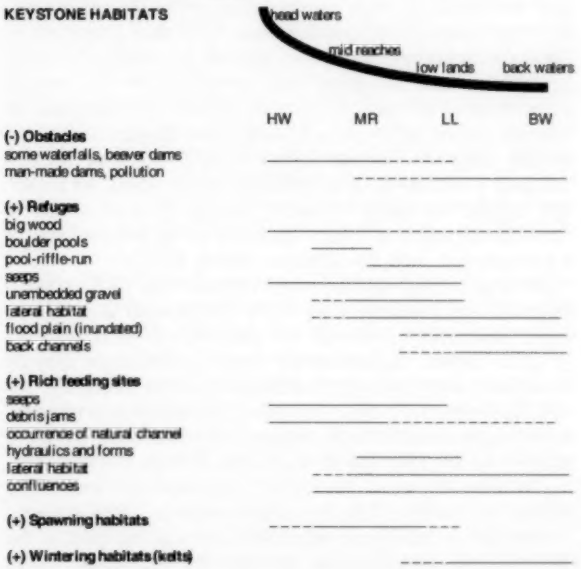

Fig. 3. Keystone habitats and their longitudinal distributions along drainage networks. Keystone habitats are grouped as obstacles, with negative effects on populations (–) and refuges, rich feeding sites and spawning habitats with positive effects on populations (+). HW, head waters; MR, mid reaches; LL, lowlands; BW, back waters.

Juvenile production is often maximal. The percentage habitat saturation (PHS; Grant 1998) is high, and fluctuations in population numbers are density-dependent. Self-thinning becomes the main regulatory factor controlling the size of the population, giving increased scope for intra-specific competition and selection.

Resilience. High resilience or the ability to recover from perturbations may be expected to characterize healthy populations. Resilience is favoured by rapid turnovers and high intrinsic rates of increase, and these will determine the ability to cope with stochastic demographic fluctuations.

Age and size structure. In healthy Atlantic salmon populations, all age classes are well represented and since age at maturity and age at migration to sea varies within the same population, there is variable, but significant, generation overlap that increases effective population size. Growth in size may be density-dependent, and stunted growth, if present, is often reversible.

Sex ratio. Factors that skew sex ratios of spawners in one direction reduce effective population size. Healthy populations will often show a variable but (on average) balanced sex ratio, roughly equal to 1:1.

Spatial distribution. Individuals within a healthy population occupy a heterogeneous environment at various spatial scales, from mesohabitats to different river reaches or tributaries. As a result the population has a high buffer capacity against exogenous disturbances, and the effect of catastrophic events is greatly reduced (risk partitioning).

Geographical distribution. Healthy populations are more likely to be found towards the center of their geographical range, where climatically-mediated habitat contractions are less likely to affect them. They are seldom isolated, and some straying from nearby streams assures a certain degree of gene flow.

(b) Genetic factors. A genetically viable population or ESU possesses genealogies that represent the evolutionary legacy of the species and the genetic variation upon which future evolutionary potential depends. The assessment of genetic viability should be directed at the monitoring and maintenance of the natural genetic diversity that reflects the local adaptation of the ESU in question. Artificial manipulation of genetic diversity and structure, or gene expression, through introductions or manipulation of the natural genetic architecture, do not serve the function of genetic health at the ESU level.

The power of genetic data rests in the large set of molecular characters generated through evolution that retain different temporal and spatial scales within the genome (allozymes, mtDNA, microsatellite loci, regulatory genes, gene expression). Assessments of genetic diversity need to use a suite of characters derived from the correct scale that

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portrays the historic and potential evolution of the species within its ESU. In any assessment, a clear knowledge of the assumptions imposed by the interpretation of patterns of genetic variation across the ESU landscape is important.

Four factors important to monitoring changes in genetic health within an ESU are identified.

Genetic diversity. Changes in genetic diversity are measured by shifts in the effective number of alleles per locus, frequency shifts in the most common allele, significant loss of rare alleles, analyses of genetic disequilibrium, and gametic disequilibrium (see Waples and Do (1994) for an explanation of terms). Temporal changes in allelic frequency in overlapping populations should be considered (Waples and Teel 1990). Analyses of changes in genetic diversity must take both genetic drift and natural changes in population structure within the ESU into account. Supplemental breeding programs frequently aim at increasing the size of a population without regard to the effects of genetic drift, which may be as important as inbreeding (Hedrick et al. 1995, Jorde and Ryman 1995). The introduction of supplemental stocks derived from fish populations from within the same ESU should be monitored for effects of genetic drift and inbreeding on locally adapted populations.

Effective population size. Monitoring the genetic viability of populations should include change in estimates of effective population size (N_e). N_e refers to an ideal population that is characterized by discrete generations, random mating, even sex ratios, where all individuals have the probability of contributing to the next generation (Waples 1990*a*,*b*). Obviously, this is not the case in wild salmonid populations. Distinctions should be made between inbreeding (N_{ei}) and variance (N_{ev}) effective numbers (Crow and Dennison 1988; Ryman 1994). There are several situations where these parameters can differ substantially based on whether a population is declining or increasing at the time of measurement (Waples and Do 1994; Ryman and Laikre 1991).

Genetic bottlenecks and founder effects. Patterns of genetic variability that document past or recent ecological and demographic events may serve as indicators of risk factors for genetic health of an ESU (Boyce 1992; Boileau et al. 1992; Lande 1993). Low levels of within- or between-population genetic variance within an ESU may indicate environmental catastrophes or anthropomorphic manipulations that have caused genetic bottlenecks and possible founder effects not detected by demographic or ecological surveys.

Reduction in population size followed by rapid growth creates conditions in which it is relatively easy for a population to shift from one co-dominant suite of genes to another (Slatkin 1996). In very small populations derived from much larger parent populations, genetic drift is the predominant factor, and it may overwhelm any selection differences among genotypes. In a rapidly growing population, after founder effect, genetic drift is relatively weak, even if the initial population is quite small, and selection will be most effective during and immediately after the period of rapid growth. Low-frequency alleles or co-adaptive complexes can be driven to fixation by selection (founder-flush) much more rapidly than they would be in populations of constant size (large or small; Slatkin 1996).

Gene flow. Natural populations tend to be subdivided to varying degrees by geographic and (or) physical barriers within their ESU that constrain movement and thus gene flow between certain populations (Rasmussen 1979; Selander 1970). Habitat choice and conspecific queuing in the context of patchy resources can result in the active aggregation of individuals with varying degrees of genetic relatedness (Barton 1995). The level of genetic differentiation and the effects of population subdivision on adaptive processes found within an ESU need direct documentation and extensive study to establish effective sampling regimes to monitor genetic health (Wade and McCauley 1988; Wade 1996).

Implementation

Anticipatory mechanisms and priorities

Protection of wild Atlantic salmon populations is a critical conservation goal. Past actions indicate that we are often in a reaction mode about addressing problems associated with salmon stocks and their habitats. Actions must be proactive to maintain the quality of the OCUs while focusing on foreseeable problems and predicting future threats. Incorporating protective measures for these anticipated events should also be considered.

Actions directed at the habitat for OCUs of Atlantic salmon should be focused on restoring and maintaining ecosystem processes that create and maintain habitats through time. It is important to insure that good habitats are identified and protected with consideration given to creating refuges in critical, keystone habitats. It is also important to maintain natural processes that account for changes to quality habitats and recognize that disturbance is an integral component of salmon OCUs in the future. It is important to educate salmon advocates and others that change is not necessarily negative. Salmon appear to be disturbance tolerant and may even require disturbance to some extent, an important subject for future research. Finally, it is important to consider the needs of other organisms in the development of a conservation plan for Atlantic salmon OCUs.

We suggest that the decision to protect an OCU considered to be in a healthy state is the first priority in a salmon conservation plan. Although the cost of such an action may be quite variable depending on context, such action may be considered low risk as the benefits in terms of biological, social, and economic values are high. Restoration and rehabilitation plans designed to recapture a previous state are more risky ventures. The cost of such work is high and the benefits in terms of social, biological, and economic values are difficult to evaluate. Finally, enhancement in order to create a new state is costly and inherently risky as the goal is, by definition, an unknown state. As funds for such conservation plans are limited, any specific plan must establish its own priorities.

Limiting commercial and recreational fisheries

Recreational and commercial catches are generally set with the intent of allowing the spawning escapement necessary to ensure future recruitment to maintain the stock. In Atlantic salmon, required spawning escapements should be related to the area available as spawning and rearing habitats, and their relative productivity. Survival and production and, therefore, the optimum spawning escapement may change in the system, either positively or negatively, due to

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any number of environmental variables. The Atlantic salmon is amenable to establishing stock-recruitment relationships for several reasons, including (1) stocks largely return to their natal river, (2) adults are not numerous and thus it is relatively easy to count them and evaluate key demographic characteristic (sex, age, weight), and (3) most of the individuals spawn once in their life. The relationship between stock and recruitment is generally modeled as a dome-shaped density-dependent relationship (e.g., Ricker 1954). Intraspecific density dependent mortality contributes to declines in survival above the optimum egg deposition (Gibson 1995). However, stock-recruitment relationships are at best noisy with density-independent variation, mainly resulting from the effects of river flows and temperatures or sea conditions, producing a wide scatter of points. As such, there is always a risk of missing management objectives by using deterministic functions describing the stock-recruitment relationship to set catch quotas.

Recently, the precautionary approach has gained acceptance as a basis for fishery management (Richards and Maguire 1998). The magnitudes of the uncertainties in fisheries management provide the principal justification for the precautionary approach. Resource managers must be advised in a way that portrays the potential consequences, or risks, of this uncertainty. In the words of Richards and Maguire (1998), an extreme interpretation of the precautionary approach could be management to such low risk that most fisheries would be closed. Conversely, management to a very high risk could lead to overexploitation at least to the point of economic extinction. The concept of the precautionary approach is included in a recent UN document of particular importance to the management of Atlantic salmon; the Straddling Fish Stocks and Highly Migratory Fish Stocks Agreement (UN 1995). Unfortunately, the number of countries ratifying the agreement is not sufficient for it to be incorporated into the Law of the Sea (Richards and Maguire 1998).

The precautionary approach appears to be the best approach to the management of Atlantic salmon stocks. The situation is serious enough that the commercial exploitation of Atlantic salmon at sea is being managed to such low risk that many interceptory fisheries are being closed or strongly curtailed. For example, in May of 1998, the Quebec provincial and Canadian federal governments announced a voluntary buy-back program aimed at eliminating the 87 Atlantic salmon fishing licenses along the north shore of the Gulf of St. Lawrence east of Natashquan, thus effectively ending commercial fishing in Québec waters. Also in 1998, the Canadian government announced a moratorium on the commercial salmon fishery in northern Labrador. In 1997, there were 205 licensed commercial salmon fishermen in northern Labrador who captured 47 t against a total quota of 50 t. Finally, the West Greenland fishery quota was reduced from 57 to 20 t in 1998.

Marine commercial fishing continues in the Northeast Atlantic. For example, in 1997, Ireland reported commercial catches of 570 t, Norway, 630 t, and the United Kingdom (England and Wales), 103 t. Current catch levels are markedly lower than in the recent past, with the 1997 catch of all homewater fisheries in the Northeast Atlantic (except Northern Ireland) below both the 1992–96 and 1987–96 means (Anonymous 1998*a*). This is believed to reflect both reductions in fishing effort and reductions in stocks. Some marine fisheries could conservatively be conducted where they can be exploited on known river stocks close to home rivers and sufficient escapement allowed for spawning and angling.

Hook-and-release angling has become a major conservation measure. In Newfoundland and the three Canadian maritime provinces, it has been mandatory to release all salmon >63 cm fork length (FL) (considered as salmon having passed 2 or more winters at sea) hooked by anglers since 1984. In New Brunswick, there is unlimited hook-and-release of kelts (salmon migrating to sea following their post-spawning, over-winter residence in freshwater) provided the angler has not taken the daily bag limit of 2 small salmon. After May 15, anglers may hook-and-release 4 salmon per day if they have not exceeded their small-salmon bag limit.

In Newfoundland and Labrador, the precautionary approach is well illustrated by the establishment of in-season reviews in 1998 to determine management directives. Prior to the July in-season review, anglers are allowed to retain only one small salmon (<63 cm FL). The Department of Fisheries and Oceans uses a traffic-light analogy to express its decisions following the in-season reviews; green light: if the in-season review indicates that returns are above or at the level of the average annual returns for the period 1992–1996, anglers would be able to retain three additional small salmon. Amber light: if the review indicates that returns are between the average annual returns for the period 1992–1996 and the poor returns observed in 1997, the single small salmon retention limit would remain in effect for the remainder of the season. Red light: if the review indicates that returns are below those observed in 1997, retention would be prohibited for the rest of the season. Hook-and-release fishing is permitted only if water temperatures do not exceed 18°C to prevent the increased mortality that occurs above this temperature (stock assessments assume 10% mortality of hooked-and-released salmon). For rivers given the green or amber light, all angling is stopped if the water temperatures exceed 22°C.

In Québec, each of its 118 salmon rivers will fall under a new, precautionary, management scheme beginning in the year 2000. The approach uses the stock-recruitment model of Schnute and Kronlund (1996) based on a parameter that determines the type of stock-recruitment curve and two management parameters: the maximum sustainable catch and harvest rate. Because of the uncertainty surrounding key population and policy parameters, the Bayes posterior probability distribution (Walters and Ludwig 1994) is applied to key parameters in order to calculate the risks of alternative management decisions to the conservation of the resource and the maintenance of local resource exploitation (Dr. P.-M. Fontaine, Fédération Québecoise pour le Saumon Atlantique, personal communication).

Finally, there is considerable discussion and controversy over the question of predator control as a means of increasing Atlantic salmon production and spawning escapement. There are 6 seal species that are considered as potential predators of salmon in eastern Canada (harp, hooded, ringed, bearded, harbor, and gray) (Anonymous 1998*b*). Although very few salmon were found in the stomachs of

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about 10 000 seals examined, seals may nevertheless represent an important source of mortality given the inverse abundance of seals and Atlantic salmon. This potential source of mortality may be more important in or near river mouths, but appropriate studies have not yet been conducted to test this hypothesis. In addition, cormorants, mergansers, and kingfishers have diverse diets, including Atlantic salmon, that reflect the broad range of species found in their habitats. Smolts appear particularly vulnerable; the diets of double-crested cormorants from all regions of Atlantic Canada combined was 17.3% Atlantic salmon during smolt runs but only 0.1% at other times of the year (Cairns 1998). The author cautions that the data are strongly biased by differential digestion rates, incomplete spatial and temporal coverage, and an over-representation of samples from salmon rivers. It appears that well-controlled experiments need to be conducted to conclusively demonstrate that predator-control programs do in fact improve salmon runs. However, the control of populations of predatory species (particularly seals) as part of a management plan to conserve Atlantic salmon is fraught with ethical problems and would surely meet with resistance from many sectors of society.

Exotics

The preservation goal of a conservation plan implies the maintenance of natural conditions within the local environment that are important to the survival of the target species (Nelson and Soulé 1987). Changes in inter- and intraspecific competition, levels of predation, and the introduction of novel diseases that occur when exotics are introduced into an ESU conflict with this goal. Exotics include introduced species, conspecific introductions from geographically and genetically divergent ESUs (see Nielsen 1994), and transgenic individuals. The natural state of ecological balance within an ESU may shift with introductions, producing subsequent shifts in the evolutionary potential of the species. All introductions must be judged on their potential impact on the evolutionary dynamics of the ESU.

Purposeful introductions of new species or conspecifics from other ESUs must be avoided. Conspecific introductions or transplantations within an ESU must fit the evolutionary strategies of the species and respect the genetic integrity of the ESU. Unintentional introductions must be eliminated as soon after discovery as possible.

Minimizing the impact of sampling methodology

Many standard methods of collecting data may have negative effects on the salmon populations we study. There is some evidence that the population of salmon under study has declined after counting fences were installed (e.g., Murray 1968). Although adult trapping facilities are valuable in long-term studies (e.g., Kennedy and Crozier 1993), less damaging methodologies should be considered where possible, such as redd counts, mark-recapture, catch-per-unit-effort in the commercial and angling fisheries and underwater observations. Handling should be curtailed by using less stressful techniques such as electronic, acoustic, or video counters. Where adults must be handled for tagging or tissue sampling, capture is best undertaken some distance upstream so that fish have had a few days in freshwater and the epidermis is thicker. Smolts are more fragile than parr and survival may be decreased by handling (Saunders and Allen 1967).

Electrofishing is effective in capturing young salmon in riffle habitats; if the proportion of catch is high, estimates by the depletion method are possible (Bohlin et al. 1989). However, the long-term effect of electrofishing on fish and invertebrates requires study. In systems where young salmon are distributed in a wider range of habitats, such as pools and lakes, electrofishing is less effective. In these habitats population estimates are better made by mark and recapture methods. A number of methods can be used to capture fish in these habitats, such as beach seine, fyke nets, trap nets, or purse seine. Where eels are abundant fyke or trap nets should not be used, since predation on the parr can be high in the traps (Gibson et al. 1987). Angling with small flies can be used to capture in situations where other methods are difficult to use (Gibson 1973), but efficiency depends very much on the skill of the angler and fry are poorly represented.

The technique of direct observation of young salmon by diving was first used by Keenleyside (1962) and is now a common method for observing behaviour and habitat use (e.g., Heggenes and Saltveit 1996). Although useful as an index, the technique may not provide accurate population estimates (Cunjak et al. 1988). Video technology is being used to extend the range of underwater observation.

Power (1993) has pointed out that the traditional method of obtaining data on diet and food consumption by wild fish is not acceptable, since it involves killing too many fish. He suggests that a physiological approach should be used to evaluate energy needs of Atlantic salmon parr in relation to temperature, growth, competition, and the food required to support production. Stomach flushing can be used to identify gut contents without sacrificing fish.

Enhancement pitfalls

The most common enhancement procedure is the supplementation of the stocks by the planting of eggs, or fry, or the release of older stages. Fry may be released unfed, shortly after "swim up," or as fed fry at some time later in the season. Young salmon may be released as parr, or "fingerlings," or they may be released as smolt, the stage at which they migrate to sea. Hatcheries are required for most of these procedures. A major problem associated with hatchery rearing is that relatively few genotypes are selected so that the genetic variability found in the natural population is not present. Another major problem is the extensive artificial selection that occurs in the hatchery environment, favouring genes that are different from those favoured by nature (Fleming and Gross 1993; Fleming et al. 1994). If fish are reared to older stages, a proportion of the young salmon die, further selecting for fish that would be less fit for natural conditions. A third problem is the direct effect on development of the phenotype (Fleming et al. 1994, 1996). To overcome some of these difficulties in rearing, the hatchery may develop a brood stock that provides progeny suitable for hatchery rearing. However, since these fish have even less genetic diversity and are more strongly under artificial selection, they are even less likely to survive in the wild. Behavioural differences between hatchery and wild salmon parr reduce their ability to survive once released (Dickson and

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MacCrimmon 1982). Furthermore, fish may be released at an inappropriate time, when suitable prey items are not available, or they may compete with and have negative effects on naturally produced fish, because the hatchery fish are bigger or more aggressive, or through competition for food or habitat. There is evidence that native salmon have been negatively affected by "enhancement" with stocking of non-native stock, which may have lacked some adaptation for the receiving river. In Newfoundland some rivers with supposedly low runs are "enhanced" by capturing wild salmon from the same river and the progeny are artificially reared so that they can be released upriver the following year. The reasoning is that survival through hatching is greater in the hatchery than in the river. However, follow-up studies must be undertaken to measure survival success of the stocked fry relative to wild fry as it is possible that no beneficial effects result. Stocking hatchery fish, or preferably introducing wild salmon, may be beneficial in the restoration of rivers that have lost their original stock.

Enhancement frequently involves opening up previously inaccessible parts of a watershed, by removing obstacles or providing fishways around the obstacle. A possible problem associated with this practice is that the fish community above the previously inaccessible barrier is likely to be changed when anadromous salmon colonize the river. In some cases species other than salmon may also be allowed access. Such waters in Newfoundland, for example, frequently have endemic populations of brook trout, landlocked salmon, and arctic char. Economically, anadromous salmon may be preferred, but biologically this could be less desirable if the endemic species are negatively affected. In addition, invertebrate and amphibian populations that require fishless habitat may be exterminated by this practice.

Enhancement may involve fertilization of lakes or streams. Oligotrophic conditions are therefore likely to become more eutrophic. This can be beneficial to increase production of young salmon (Gibson and Haedrich 1988), especially in regions where there is a depauperate fish fauna, so that competing species would not be enhanced. However, the plant and invertebrate communities are changed, so that although fish production is increased, the stream may no longer be regarded as "healthy."

Communication

If human activities are to be sustainable, we need to ensure that the ecological systems on which our economies depend are resilient. Arrow et al. (1996) recommend institutional reforms that would compel private users of environmental resources to take account of the social costs of their actions. The problem involved in devising environmental policies is to ensure that resilience is maintained, even though the limits on the nature and scale of economic activities thus required are necessarily uncertain. They emphasise the need for reforms that would improve the signals that are received by resource users. Harte (1996) assesses the two generally held views of future development, one of which is that nature is the ward of humanity and the other that it is the steward. He believes that the common sense values underlying the nature-is-steward vision are not being communicated adequately to the public. He claims that we are losing the educational battle because the science underlying the nature-is-steward vision does not appear to be as convincing, let alone as dazzling, as is the science underlying the people-are-stewards vision of continuing growth and of conversion of wild habitat to manacled rivers and manicured forests. It is in the global interest to keep as much biodiversity as possible at the genetic, species, and ecosystems levels (Fuentes-Quezada 1996).

Although loss and degradation of habitats, and harvesting, are acknowledged to be the major negative factors that have caused the demise or decline of salmon stocks, enforcement of regulations is weakly applied unless there is "political will" or, in other words, public awareness and public political pressure. A relatively minor example of the advantages of public interest, but repeated in other areas in the last decade, could be the city rivers of St. John's, Newfoundland. Up to 15 years ago fisheries regulations concerning habitat were consistently ignored, wetlands were filled in, streams channelized or put underground, riparian vegetation removed for developments, and storm sewers, with added effluents, discharged directly into streams (Gibson and Haedrich 1988; Steele et al. 1993). Environmental groups then fought to control the destruction and with political pressures ensured that habitat regulations were enforced, and enhancement programmes have followed. After several years of government lobbying, a local group received permission to stock salmon as fry, which are thriving and salmon runs are likely to be restored. The example has encouraged other municipalities on the island to follow suit. The environmental movement concomitant with public education on the values of habitats has slowed loss of habitats across the country, and improved waters in some areas.

In discussing the philosophy of ecosystem management and the necessity of public education and communication, Schramm and Hubert (1996) suggest that the concepts of optimum sustained yield and ecosystem management are similar. Ecosystem management involves changing the spatial and temporal scales of management from a focus on the local scale and immediate benefits to broader geographical scales (the entire watershed and beyond) and long-term benefits. There must be a collaborative approach involving a diverse array of stakeholders. Communication among resource managers and their agencies is necessary. Communication within agencies is necessary, and managers and field staff must understand the philosophy, how to implement it, and how to communicate with and raise input from the public.

The research conducted to develop our understanding of salmon ecology must also be communicated to the general public to foster public awareness of the value of conservation. Public lectures, articles in the popular press, public involvement in research projects and general visibility of scientific research are all means to heighten public understanding of natural ecosystems. Such understanding is essential if the public is to be expected to support the biological and societal values of nature, rather than economic exploitation, and apply the political pressure necessary to preserve natural resources.

Research strategies

To fill the gaps in our knowledge about Atlantic salmon and their habitats and to implement meaningful conservation plans, we should consider changing the way we do research.

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In particular, we must develop networks of multidisciplinary and international research groups working together on common goals. Collaboration among university, government, and industry to set up such networks is essential, permitting access to public research funds that are increasingly targeted to such efforts. Furthermore, such networks are important tools for advocacy, providing the visibility and impact necessary to influence public opinion and hence, government policy. Although the efforts of individual research laboratories remain the backbone of the scientific enterprise in most countries, collaboration offers the promise of significant advances in knowledge beyond the reach of individual laboratories.

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Physiological Changes Associated with the Diadromous Migration of Salmonids

Helga Rachel Høgåsen

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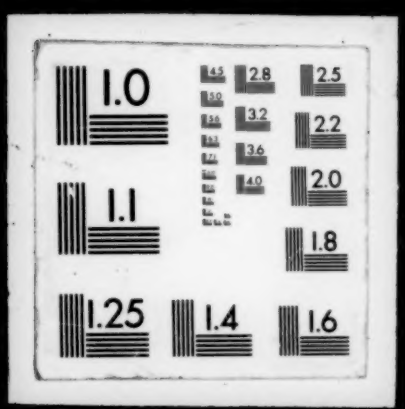
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